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The Sexual Development of Domestic Turkeys Exposed to Light Regimens Simulating Three Seasonal Photoperiods[1]

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THE DOMESTIC turkey, akin to the wild turkeys and other species of nonmigratory birds, normally will limit its reproductive activity to the spring months. Light has been demonstrated to be the most important single factor determining the reproductive pattern in these species (cf. reviews by Farner, 1959, and Lees, 1960).

Accordingly, numerous investigators in recent years have sought ways to alter this reproductive pattern in the domestic turkey (e.g., Garland *et al.,* 1961; Leighton and Shoffner, 1961 and 1964; McCartney *et al.,* 1961; Harper and Parker, 1962; Polley *et al.,* 1962; and others). This effort has been encouraged by the need of the turkey industry to meet a steadily growing demand for off-season hatching eggs. In general, the research approach chosen by these investigators has involved determination of optimal lighting schedules, both for growing and breeding phases, best capable of maximizing the reproductive potential of the turkey. Such an approach, logical as it is for the solution of a pressing practical problem, has largely by-passed another important aspect of photoperiodism in the domestic turkey: its response to what may be referred to as the annual, natural lighting cycle. The purpose of the present investigation was to study an aspect of the problem by means of an experimental design in which this cycle was, as nearly as possible, simulated under controlled conditions.

Materials and Methods

The poults used in the study were hatched May 1, 1959, from two Washington State University lines of Broad Breasted Bronze turkeys genetically isolated since 1954. The lines were: line 1—a nonselected, random-bred, population, and line 3—a population selected, on an individual and family basis, for high egg production.

Following hatching, individually wing-banded poults were sexed and assigned, on the basis of a restricted randomization, to 12 groups each having

[1] Scientific Paper No. 2456, Washington Agricultural Experiment Stations, Pullman. Project 717. This investigation was supported in part by federal funds for regional research (W-7) under the Hatch Amended Act.

32 poults. Each group was homogeneous with respect to sex and line. The experimental design called for three treatments which were to provide the poults with photoperiods simulating the number of hours of natural light the poults would receive during adolescence, if hatched at one of the three different times of year: on December 21 (treatment 1), March 21 (treatment 2), and June 21 (treatment 3). The light regimens for each treatment followed the daylight hours appropriate for a northern latitude corresponding to that of Pullman (46° 44′). The "daylight" hours available to each of the three treatment groups are shown in Figure 1. However, for reasons totally unrelated to the original design of the study, during the first three weeks after hatching the poults had to be kept in battery brooders and subjected to a uniform regimen of 12 hours of artificial light per day. On May 23, 1959, the poults were randomized in 12 experimental pens, and the appropriate light treatments were initiated. Each pen, measuring 7 x 14 feet in floor area, was completely enclosed and was lighted by a single 200-watt incandescent bulb located near the ceiling. Light intensity was found to be approximately 30 foot candles at the bird's back. Time clocks governing the hours of light were adjusted once a week. The ambient temperature within the pen was approximately the same, $\cong$ 75° F, maintained by a common forced-draft ventilation system. For the first four weeks following the transfer of the birds to the experimental pens, the two sexes, due to space limitations, were housed together. After that, for the balance of the prebreeding phase, the sexes were separated. The birds remained exposed to their respective lighting systems for at least 30 weeks. Water and appropriate feed were available to the birds *ad libitum.*

The distribution of the 12 experimental groups among the three light treatments perhaps can best be visualized by referring to the following tabulation:

	Line 1		*Line 3*	
	Males	*Females*	*Males*	*Females*
Treatment:	1, 2, 3	1, 2, 3	1, 2, 3	1, 2, 3

Starting June 12, two birds were taken at random from each pen at approximately two-week intervals to provide data on gonadal development. These birds were first weighed individually and then sacrificed by severing the carotid artery. (The blood from each bird was collected to provide data for another phase of the study to be reported elsewhere.)

The gonads, the left and the right testis or the left ovary, were removed and weighed. The testes were then fixed in Bouin's solution to preserve

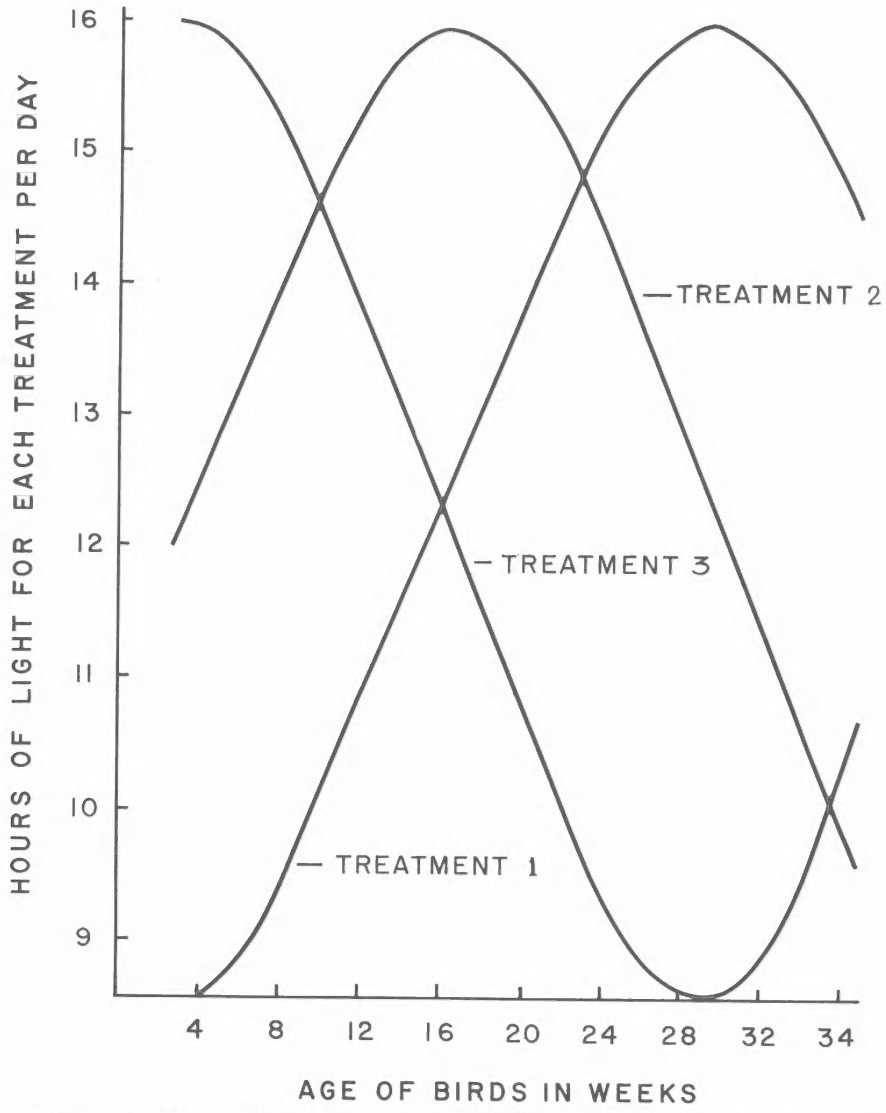

Figure 1. Hours of artificial light, received by birds, according to age and treatment.

them for future histological examination. The latter, aside from providing information on progressive changes within the testes, also permitted measuring the diameter of the seminiferous tubules. Representative sections of a single testis were collected on a slide. The diameter of three seminiferous tubules per section was measured with the aid of an ocular micrometer, with three

sections being measured per slide. Thus, a total of nine measurements were made on each testis. Starting September 4, the males, then 16 weeks old, were examined at weekly intervals by the method of Carson *et al.* (1955) for the presence of spermatozoa in the cloaca: three males, taken at random, per treatment and line classification provided the necessary information. This procedure continued until the presence of massed spermatozoa indicated that the males were sexually mature, i.e., they were considered capable of effective mating. In this examination, *all* males of a given group were regarded to be sexually mature when respective three-male samples from that lot showed spermatozoa in the cloaca for two consecutive weeks.

As none of the females had started laying eggs by the age of 38 weeks (on January 26, 1960), 10 females, taken at random from each pen, were moved to a regular turkey breeding house provided with windows along the front. Each such group was mated to a sexually active male, obtained from a reserve male turkey flock, and exposed to 14 hours of artificial light per day. A daily pen record of egg production was kept for the subsequent 13 weeks.

Results

In general, the left testis was found to be heavier than the right, regardless of the treatment or line (Table 1). On the other hand, because the side

TABLE 1. WEIGHT OF LEFT AND RIGHT TESTES, EXPRESSED IN GRAMS PER KILOGRAM OF BODY WEIGHT (treatment and line classification disregarded)

	Age in Weeks									
Testis	6	8	11	13	17	19	23	27	29	33
Left	0.018	0.047	0.062	0.097	0.162	0.184	0.202	0.425	0.446	1.341
Right	0.013	0.025	0.030	0.049	0.081	0.100	0.104	0.218	0.155	0.861

from which the gonad came had no detectable effect on testis response to treatment, detailed comparisons of the relevant data were limited to the left testis (Figures 2, 3, and 4).

It is apparent from Figure 2 that exposing males to a lighting schedule that approximated the increasing hours of natural daylight following the winter solstice (treatment 1) resulted in a reasonably steady rise in the size of the testis. When the presence of spermatozoa in the cloaca was used as the criterion for classifying the male as being "sexually mature," it was found that all males in treatment 1 could be classified "positive" by the time they reached the age of 24 weeks (Table 2). In fact, some of these males had cloacal spermatozoa as early as the 19th week.

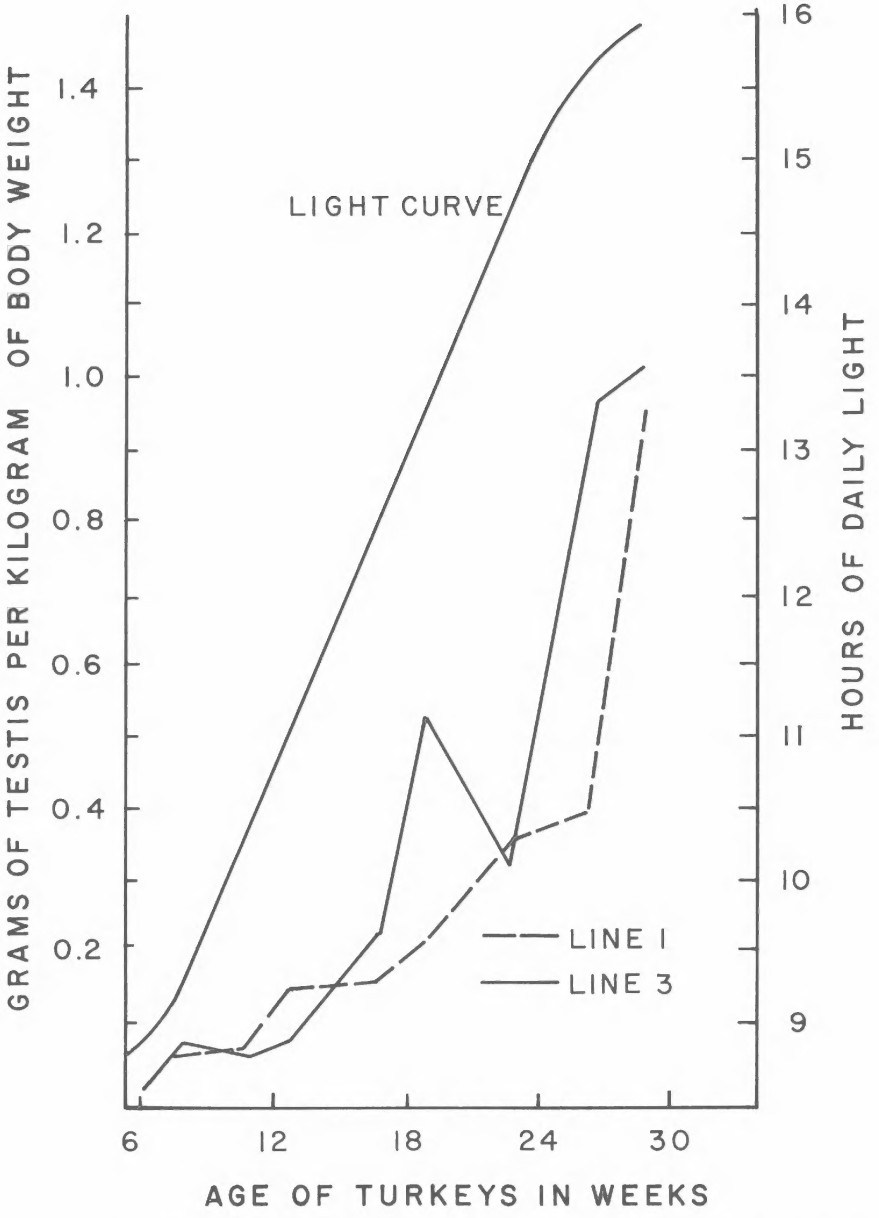

Figure 2. Weight of left testis in relation to age of birds and daily light exposure. Treatment 1.

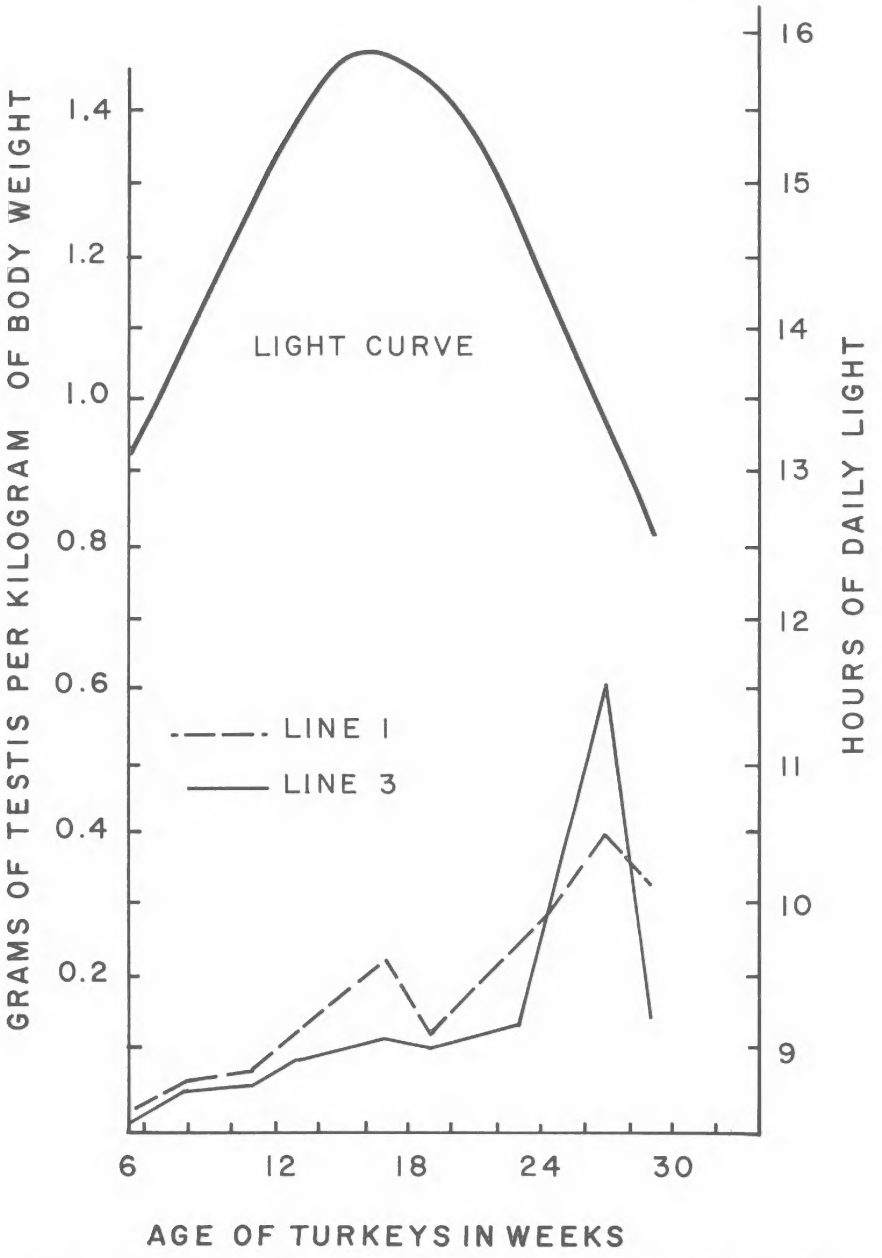

Figure 3. Weight of left testis in relation to age of birds and daily light exposure. Treatment 2.

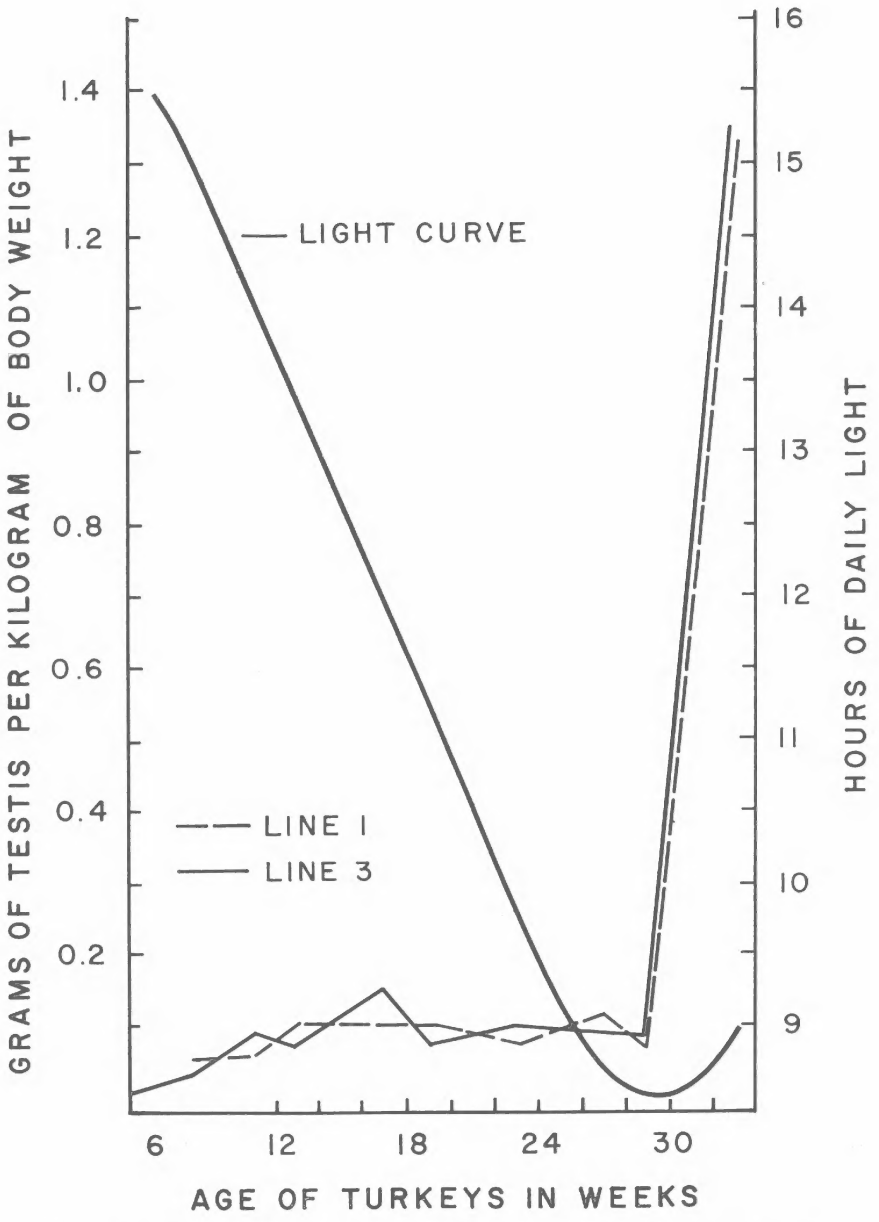

Figure 4. Weight of left testis in relation to age of birds and daily light exposure. Treatment 3.

TABLE 2. PRESENCE OF SPERMATOZOA IN THE CLOACAE OF MALE TURKEYS, BY LINES, TREATMENTS AND AGE OF THE BIRD

Treatment	Line	Male No [a]	Age in Weeks: 16	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34
			9/4	9/11	9/18	9/25	10/2	10/9	10/16	10/23	10/30	11/6	11/13	11/20	11/27	12/4	12/11	12/18	12/25
1	1	1	—[b]	—	+	+	+	+	++[d]										
		2	—	+[c]	+	+	+	+	++										
		3	—	—	—	—	+	+	++										
	3	1	—	—	+	+	+	+	++										
		2	—	—	—	+	+	+	++										
		3	—	+	+	—	+	+	++										
2	1	1	—	—	—	—	+	+	—	+	+	+	++						
		2	—	—	—	—	—	—	+	+	+	+	++						
		3	—	—	—	—	—	—	+	—	+	+	++						
	3	1	—	—	—	—	—	+	+	+	+	++							
		2	—	—	—	—	+	+	+	+	+	++							
		3	—	—	—	—	—	+	—	+	+	++							
3	1	1	—	—	—	—	—	—	—	—	—	—	—	—	+	—	+	+	++
		2	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	++
		3	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	++
	3	1	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	+	++
		2	—	—	—	—	—	—	—	—	—	—	—	—	—	+	+	+	++
		3	—	—	—	—	—	—	—	—	—	—	—	+	+	—	+	+	++

[a] Different males were chosen, at random, each week.
[b] — Spermatozoa absent.
[c] + Spermatozoa present.
[d] ++ All males in the treatment group were considered to be sexually mature; no further observations were made.

The lighting schedule of first rising and then declining number of daylight hours (treatment 2), a pattern found in nature subsequent to the vernal equinox, yielded a growth curve for the testes that, in general, showed the same trend as that exhibited by the light curve (Figure 3). Compared with treatment 1, the first appearance of identifiable spermatozoa in treatment 2 birds was delayed by two weeks. However, once initiated, sperm production continued unabated despite the fact that at the time first spermatozoa were identified in the cloacae of these males, the lighting schedule had been in the declining phase for nearly eight weeks.

In treatment 3, the testes showed almost no growth, relative to body size, until the birds were 29 weeks of age. It will be recalled that the lighting schedule in that treatment approximated the pattern of daylight—darkness distribution found in nature after the summer solstice (June 21). As can be seen in Figure 4, a *spectacular* increase in testis size occurred at the age of 29 weeks, coinciding with the first detection of spermatozoa in the cloaca (cf. Table 2).

As no side or genetic line effect could be detected with respect to the diameter of the seminiferous tubules, the relevant data were combined and compared by treatment only (Figure 5). These data are seen to reflect to a considerable extent a pattern similar to that already presented in Table 2 regarding the spermiogenic response to the light regimes. The beginning of rapid increases in the seminiferous tubule diameter at 17 and 19 weeks of age in treatments 1 and 2, respectively, preceded the first appearance of the spermatozoa in the tubules and in the cloacae. The increase in the tubule diameter in treatment 3 males was more gradual until the extremely rapid growth that occurred between the 29th and the 33rd week. There is little doubt that even in the presence of considerable variability within the observed specimens, the curves reflect biologically significant treatment-induced differences in the pattern of size increments of the seminiferous tubule diameter.

Because the data on ovary weight showed no differences that could be ascribed to line effects, the line classifications were disregarded (Figure 6). It can be seen that a reasonably close similarity existed between the responses obtained from treatment 1 and 2 birds. In treatment 3, a steady, though somewhat slower, increase was observed in the weight of the ovary (in relation to body weight) contrasted with the steadily decreasing "day length" during the corresponding observational period (cf. the light curve in Figure 4). The anatomical and physiological development represented by this growth was reflected in the rapidity with which treatment 3 birds reacted to an

increase in the daily light regimen to 14 hours: days to the first egg in treatment 1, 2, and 3 groups were 23, 15, and 8, respectively.

Both line and treatment differences became apparent when the 13-week egg-production period was examined (Table 3). One sees, for example, that following the initiation of the uniform "14-hour day," line 3 treatment 3 birds, i.e., hens from a line selected for egg laying and raised to 28 weeks of age on a gradually decreasing light regimen, proved to be superior both in regard to days to first egg and rate of egg laying. The average egg production of that group for the 13-week period was 59.9 per cent, nearly 6 per cent above the corresponding figure for genetically comparable treatment 1 and 2 hens. Using "Student's" method for paired observations, this difference was found to be statistically significant at the 5 per cent level.

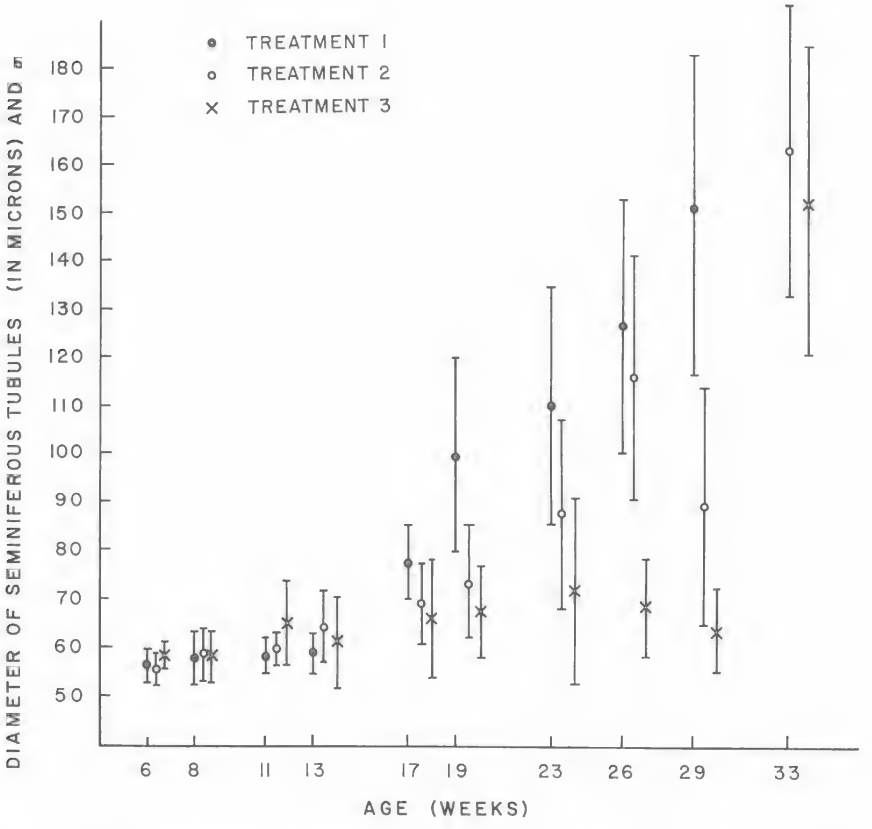

Figure 5. Diameter of seminiferous tubules in relation to age of birds and treatment.

A 16 per cent difference existed within treatment 3 groups, between line 1 and line 3 hens with respect to egg laying: 44 vs. 60 per cent, respectively. Again, this difference was statistically significant at the 5 per cent level. Nearly as great a difference in the average egg lay was recorded for line 1 and line 3 birds in treatment 2: 41 vs. 54 per cent for the two groups, respectively ($P<0.05$). No such difference was observed between the two lines in treatment 1.

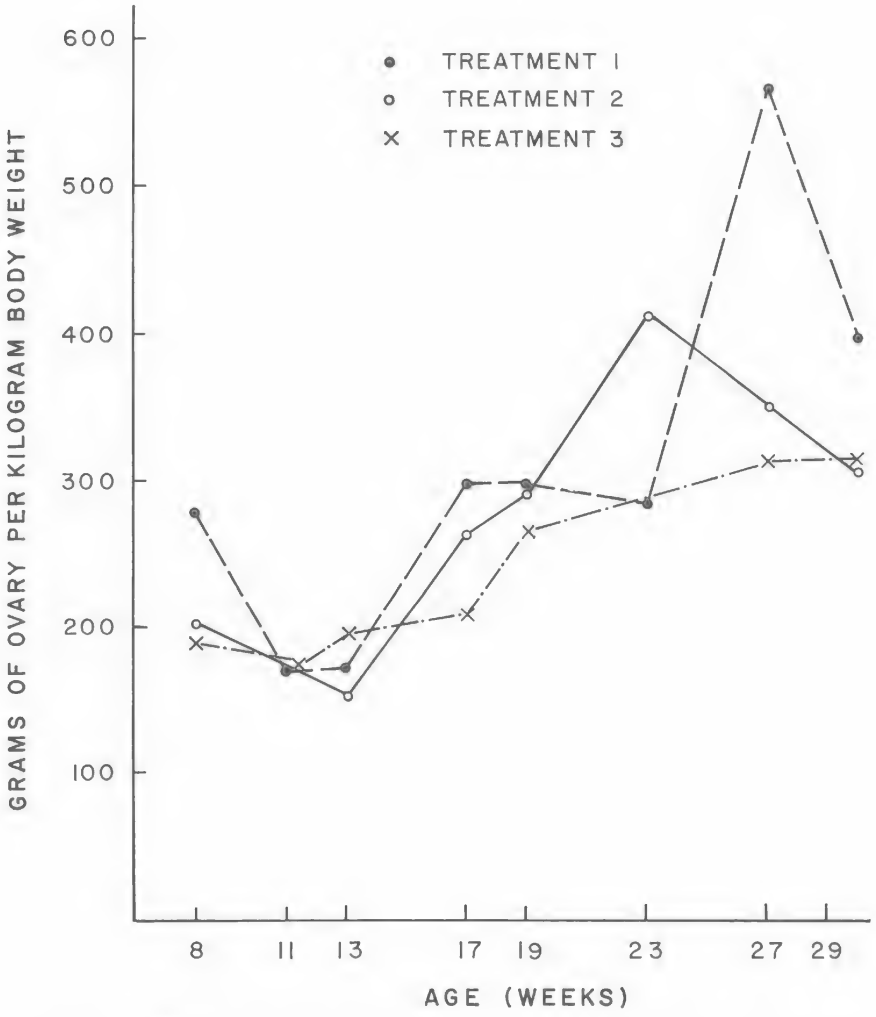

Figure 6. Weight of left ovary in relation to age of birds and daily light exposure.

TABLE 3. Per Cent Weekly Egg Production by Lines and Treatments

Production in weeks	Age in weeks	Treatment					
		1		2		3	
		Line 1	Line 3	Line 1	Line 3	Line 1	Line 3
1[a]	38	00.0	00.0	1.4	00.0	15.7	5.7
2	39	00.0	00.0	17.1	8.6	62.9	67.1
3	40	5.7	5.7	42.9	45.7	74.3	97.1
4	41	45.7	42.9	55.7	55.7	65.7	91.4
5	42	51.4	51.4	41.4	65.7	51.4	67.1
6	43	54.3	51.4	40.0	64.3	37.1	58.6
7	44	54.3	64.3	50.0	61.4	40.0	62.9
8	45	67.1	65.7	50.0	65.7	61.4	55.7
9	46	68.6	62.9	59.4	60.0	54.3	68.6
10	47	68.6	67.1	47.6	57.1	41.4	54.3
11	48	51.4	65.7	46.0	61.4	25.7	55.9
12	49	55.7	61.4	42.9	55.7	20.0	50.8
13	50	56.7	51.4	38.1	41.4	21.4	42.9
$\overline{X}$		52.7	53.6	41.0	53.6	43.9	59.9

[a] Following the initiation of 14 hours of light per day.

Discussion

Light is the factor responsible for the onset of functional reproductive capacity of the male domestic turkey. This is the principal conclusion that emerges from the results of our study in which possible involvement of such variables as date of hatch (i.e., season) and of population genotype was removed from the experimental design, in which length of daily exposure to light was the only known major variable. This supports the conclusion reached by McCartney *et al.* (1961) and Polley *et al.* (1962) that the exposure of young turkey males to large daily doses of artificial light does not depress the course of their sexual development.

These results are based on a reasonably close agreement between the long-term pattern of daylight hours, as represented by the three treatments used in the present study, and the prevalence of positive tests for the presence of mature spermatozoa in the male cloaca.

Examination of Table 2 reveals that spermatozoa were first identified in some treatment 1 males ("hatched December 21") as early as 19 weeks of age. Three weeks later all of the birds examined in that group were considered to be positive to the test. It will be recalled that these birds had been exposed to a steadily rising day length from the date the controlled lighting program was instituted three weeks after hatching. A reference to Figure 2 will also show that there was agreement in the direction of the slope of the light curve and that of the testis weight (when the latter was expressed in relation to body weight). A similar seasonal pattern in the light dependence of the testis size in the starling was demonstrated over 30 years ago by Bissonnette (1930). The latter finding laid the foundation for much of the subsequent work on photoperiodism in wild birds. A rising and then diminishing daylight curve for treatment 2 birds ("March 21 hatch") resulted in five- to six-week delay in the onset of functional reproductive capacity; the corresponding condition was not reached in treatment 3 birds ("June 21 hatch") until some four weeks later.

A significant fact about treatment 3 birds was that even on a rapidly diminishing light regimen, in effect until the birds were 30 weeks of age, at least one 29-week-old male gave a positive test for the presence of spermatozoa in the cloaca. It will be seen by referring to Figure 4, that by then the males had been receiving less than 10 hours of daylight for at least six weeks. This either demonstrated the cumulative effect of prior, massive photostimulation (cf. Wolfson's "Summation Hypothesis" in his 1952 paper, according to which "the amount of light which a bird received each day or

the total amount within a given period of time might determine the time of response") or, simply, the existence of an "innate" capacity of the testis to reach a reproductively functional state (cf. Vaugien, 1953, and Magsood, 1954). A rapid response of treatment 3 birds even to a slight (less than 1 hour) increase in day length above the minimal day of 8.5 hours showed them to be physiologically ready for reproductive activity. This was accompanied by a dramatic increase in gonad size (cf. Figure 4).

It is possible, of course, that the latter can be attributed, at least in part, to the maintenance of uniformly temperate ambient temperature for these birds throughout the time during which they were subjected to gradually altered photoperiods. Even though earlier evidence (e.g., Kirschbaum and Ringoen, 1936; Kendeigh, 1941) pointed to the apparent lack of temperature effect on reproductivity in seasonally breeding species of wild birds, more recent studies (e.g., Engels and Jenner, 1956; Farner and Wilson, 1957; Snow, 1958) suggest that extremes of temperature depress reproductivity in such birds. Similar evidence for the domestic turkey has been reported from this laboratory (Law and Kosin, 1958).

The condition of refractoriness to light in the turkey males just reaching sexual maturity was not evident in the present study. This was not entirely surprising because a study by Law and Kosin (loc. cit.), in which the sperm-producing capacity of turkeys was examined over a two-year period, showed that under an adequate lighting regimen, a turkey male can remain reproductively active beyond a single 12-month period. Furthermore, Ogasawara and Asmundson (1959), McCartney *et al.* (1961), and Polley *et al.* (1962) showed that turkey males have little or no "dark dependent" requirement for the initiation of semen production. In this respect, the turkey male resembles the drake which, according to Benoit *et al.* (1956), can pass through at least two breeding seasons without showing any signs of refractoriness.

By contrast, the female turkey approaching her first breeding season will, if appropriately preconditioned, exhibit refractoriness. The latter can be achieved by exposing the maturing female to increasingly longer photoperiods either of natural or artificial light (e.g., Clayton and Robertson, 1962; McCartney *et al.*, 1961; Harper and Parker, 1962). This proved to be true also in the present study in which, as it will be recalled, the pattern of daylight hours in the three treatment groups of poults, all hatched on the same day, was set by three widely separated calendar dates: December 21, March 21, and June 21.

In this connection, a possibly significant observation was that in treatment

1 birds the initial depression of egg laying affected equally both genetic lines used in this study: neither line overcame the handicap imposed by the initial refractoriness (Table 3). In the case where refractoriness did not prove to be a major factor affecting oviposition (in treatment 2), or where it was not evident (in treatment 3), the genotypic difference between the two lines for egg laying was clearly expressed. This would suggest that refractoriness in turkeys should be amenable to selection. The domestic chicken, which as a result of selection is no longer a seasonal reproducer as the turkey still is, shows little if any evidence of refractoriness (e.g., Morris and Fox, 1958).

Summary

1. Male and female poults of the Broad Breasted Bronze variety of turkeys and representing two genetically isolated lines (a random-bred line and a line selected for egg laying) were hatched May 1, 1959. At three weeks of age the poults were subjected to one of three light treatments: treatment 1 which duplicated the light pattern birds would encounter in nature if hatched on December 21; and treatments 2 and 3 which represented the corresponding light conditions subsequent to March 21 and June 21, respectively. The birds were raised in *complete* confinement. Periodic observations were made on testis size, seminiferous tubule diameter, presence of spermatozoa in the male cloaca, and size of the left ovary by lines and treatments. The females, when 38 weeks of age, were placed on 14-hour days, and egg-laying records were kept, by treatment and lines, for the subsequent 13 weeks.

2. The males showed no refractoriness to light, regardless of the experimental light treatment used both during their adolescence and immediately prior to the onset of sexual maturity. (The latter was determined by the presence of morphologically mature spermatozoa in the male cloaca.) Sexual maturity was reached first by treatment 1 males, followed by treatment 2 males and treatment 3 males, in that order.

3. Female birds, subjected to massive exposure to artificial light in the latter part of their growing period (treatments 1 and 2), exhibited definite signs of refractoriness. Furthermore, there was evidence of genetically induced differences with respect to the degree of observed refractoriness. The latter points to a possibility of selecting against light refractoriness in the domestic turkey.

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Tertiary Plant Fossils from the Methow Valley, Washington

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THE PIPESTONE formation is a stratigraphic unit within the Methow-Pasayten Graben, a peninsula of sedimentary rock which extends southward from Canada into north-central Washington (Figure 1). It crops out in a series of three fault blocks which begins about five miles northeast of the town of Twisp, Washington, and extends southwestward for several miles. The northernmost fault block was dissected by Pleistocene glacial waters forming the Pipestone Canyon which has been designated stratigraphic type locality of the formation (Barksdale, 1948).

The geologic section of the Pipestone formation consists of about 2,000 feet of interbedded conglomerates, arkosic sandstones, siltstones, and shales. Along their western margin these rocks unconformably overlie or are in fault contact with lower Cretaceous rock of the Newby formation and in the north, east, and south are in fault contact with Mesozoic crystalline rocks of the Okanogan Complex. The formation was named and described by Barksdale (1948), and a detailed lithologic and stratigraphic study was conducted by Ryason (1959). A provisional age of Cretaceous-Tertiary was assigned to the formation by these workers based on stratigraphic relationships which, combined with its relatively little-deformed "youthful" appearance, indicate that it is the youngest formation within the Methow-Pasayten Graben.

Scope of Study

This study involves a problem which has plagued students of North American stratigraphy for nearly a century: recognition of the Cretaceous-Tertiary boundary. Significant contributions toward the solution of this problem have been made through paleobotanical studies (Brown, 1962). A study of the fossil flora of the Pipestone formation was undertaken in an effort to determine its age on the basis of established paleobotanical relationships.

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Carbonized plant remains had been reported from the formation previous to this study. Ryason (1959) illustrates two fossils which he calls *Parataxodium* and *Nymphaeites.* The present study, however, constitutes the first attempt to obtain and describe a representative floral assemblage from the formation. Collections for this study were made in the fall of 1960 from the middle beds of the formation at the type locality.

Floral List

Metasequoia occidentalis (Newberry) Chaney.
Taxodium dubium (Sternberg) Heer.
Cercidiphyllum arcticum (Heer) Brown.
Dillenites sp. cf. *D. ellipticus* Hollick.
Platanus raynoldsi Newberry.
Pterospermites sp. cf. *P. spectabilis* Heer.
Vibernum antiquum (Newberry) Hollick.

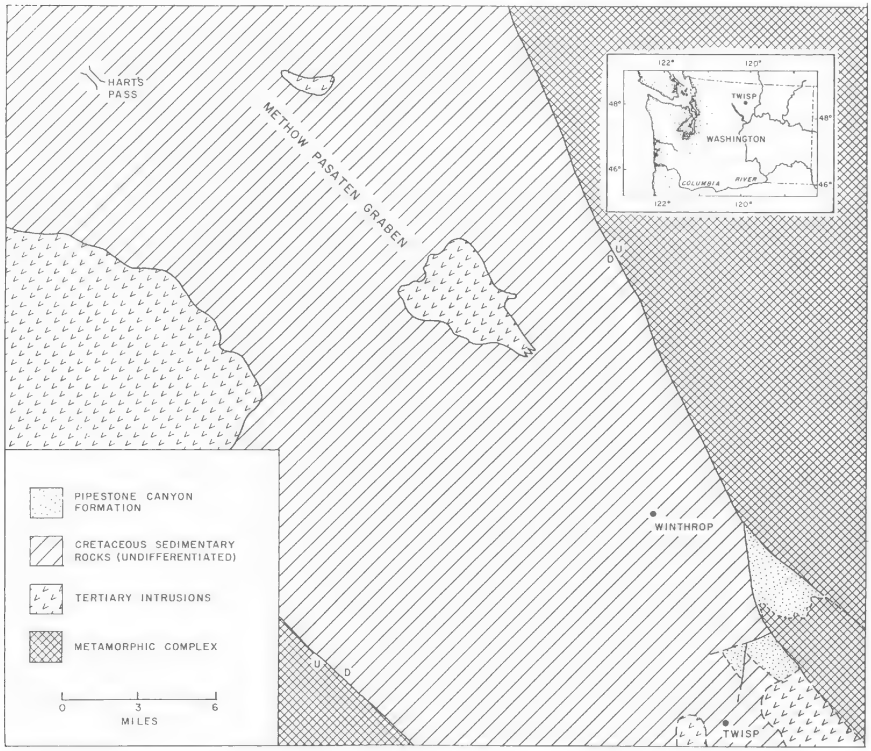

Figure 1. Geologic map indicating the relationship of the Pipestone formation to adjacent rock units (simplified after Barksdale, unpublished data).

Floral Discussion

The small size of this collection and the few species present do not justify statistical comparison with other floras. Only general relationships involving the occurrence of species and their general abundance will be considered. References cited in the bibliography should be consulted for detailed taxonomic descriptions.

All species identified from the Pipestone formation have been recorded from the Tertiary of Alaska, and all except *Dillenites* sp. occur in Cretaceous and Tertiary rocks of the western interior of Canada and the United States.

Reference to the conifer *Metasequoia* is infrequent prior to 1950, but it now is believed to have been nearly ubiquitous throughout the higher latitudes during Cretaceous and early Tertiary times. Massive compactions of deciduous short-shoots and female cones of the Tertiary form, *M. occidentalis,* are abundant in rocks of the Pipestone. The type specimen of this species comes from the Chuckanut formation near Bellingham, Washington, which is considered to be of Paleocene age. *Taxodium dubium* is far less abundant than *M. occidentalis,* but Chaney (1951) has noted that in floras where *M. occidentalis* is abundant, *T. dubium* is commonly sparsely represented. Both have been reported from the Latah formation and from beds near Republic, Washington (Knowlton, 1926, and Brown, 1936).

Specimens of *Cercidiphyllum arcticum* from the Pipestone are less deltate than forms illustrated by Brown (1962) from the Rocky Mountains and Great Plains of the western United States. They bear a striking resemblance to leaves figured by Baykovkaya (1956) from east-central Siberia which he assigns to *Trochodendroides richardsoni,* a species included by Brown in his synonymy of *C. arcticum.*

Fragmented specimens which resemble *Dillenites ellipticus* figured by Hollick (1936) from the Alaska Tertiary are of minor occurrence. Brown (1962) suggests that the four species of *Dillenites* described by Hollick may actually represent a single species. Because of this uncertainty, specific identification of Pipestone specimens is of minor concern.

The aquatic species, *Nymphaeites angulatus,* is commonly preserved in rosette form and has been widely reported from both Cretaceous and Paleocene rocks of North America. Although it is a distinctive form, it has a lengthy synonymy resulting from disagreement among workers on taxonomic details. Newberry first examined single leaves of the species which he assigned to *Neuropteris angulata.* Subsequent study of the entire rosette caused Lesquereau to designate the form as *Trapa microphylla.* Bell (1949) observed

that the veination did not terminate craspedodromously in the marginal teeth, as indicated by Lesquereau, but in a submarginal vein. He thus redescribed the species as *Nymphaeites angulatus,* retaining the specific name given by Newberry. Most recently, Brown (1962) has included *N. angulatus* in his synonymy of *Trapa angulata.* Since *Nymphaeites angulatus* appears to have received the widest usage, it has been retained in this paper. It may be considered synonymous with *T. angulata.*

Several large suborbicular leaves have been referred to *Platanus raynoldsi.* The broad, strong double dentation, cuneate base, veination, and large size make the species distinctive. Specific assignment of large ovate leaves to *Pterospermites* is less certain. Specimens compare favorably with *P. spectabalis* illustrated by Hollick (1936), but the subopposite character of the basal primaries is the only feature distinguishing them from *P. alterans.* Minor variations in margin, base, and apex of specimens make assignment to a single species difficult. Leaves of this type have not been widely reported, and there appears to be considerable doubt as to the generic and specific relations of those reported to date. Hollick (1936) illustrates this uncertainty in saying that, "the stratigraphic probability appears to be that Cretaceous forms of these closely related large leaves may properly be referred to *Protophyllum, Pseudoprotophyllum* or *Crednaria* and Tertiary forms to *Pterospermites* or *Grewiopsis."* This indicates that generic placement of such leaves depends in part on a knowledge of the stratigraphic age of beds in which they are found. Comparison of Pipestone specimens with leaves of Tertiary assemblages is, however, favorable.

Vibernum antiquum constitutes nearly half the broad leaves taken at two fossil localities. It is reported that certain localities in the Ravenscrag, Lance, and Fort Union formations show similar occurrence of this species. A few specimens from the Pipestone may represent *V. asperum*, but because of their association with a greater number of leaves assigned to *V. antiquum,* they are included with the latter.

Conclusions and Age

Although the eight species which constitute the Pipestone assemblage range from late Cretaceous well into the Tertiary, the only epoch common to all is the Paleocene (Figure 2).

Cercidiphyllum, Platanus, Metasequoia, and *Taxodium* indicate temperate climatic conditions, and the neotropical genera *Dillenites* and *Pterospermites*

suggest warmer conditions encountered along the southern margin of the temperate zone. Thus the Pipestone flora appears to represent a warm-temperate phase of the Arcto-Tertiary flora. Ectotomes of this type in southern British Columbia, central United States, and in Europe have been noted by Chaney (1947).

The character of the Pipestone flora compares most favorably with early Tertiary floras of Alaska and the western interior of Canada and the United States. By merit of these relationships, the Pipestone formation should be considered to be of Paleocene age.

Acknowledgements

The writer expresses his thanks to J. D. Barksdale and V. S. Mallory of the University of Washington for encouraging this writing, providing helpful suggestions on preparation of the plates, and reviewing the manuscript. Particular thanks is extended to J. S. Lowther of the University of Puget Sound for his guidance and interest in this study. Dr. Lowther is presently engaged in an extensive study of plant fossils of the Methow Valley to which this work may constitute a minor contribution.

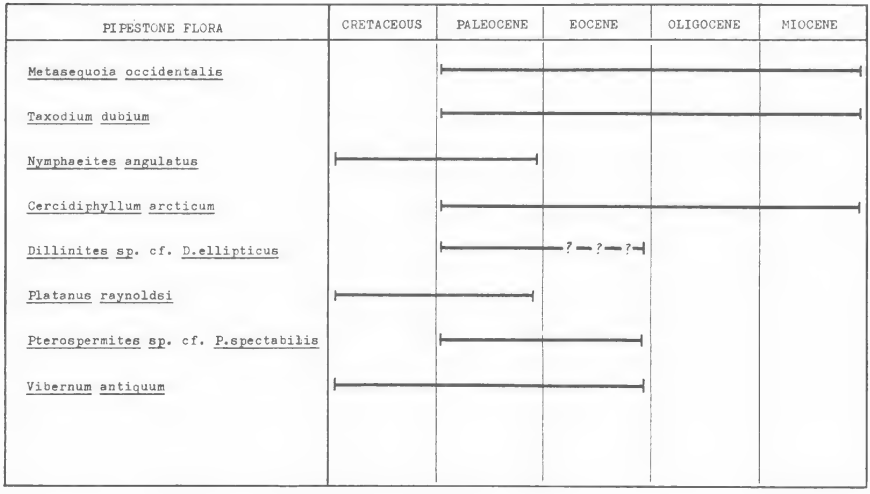

Figure 2. A chart indicating the geologic ranges of species of the Pipestone flora. Tertiary ranges are after LaMotte (1952). A late Cretaceous occurrence of *N. angulatus* is reported by Bell (1949) and of *V. antiquum* by Berry (1935). A Cretaceous variety of *P. raynoldsi* is reported from the Edmonton formation by Bell (1949), and Brown (1962) also suggests a Cretaceous genesis of this species. Because of these uncertainties, a Cretaceous range is allowed here for *P. raynoldsi.*

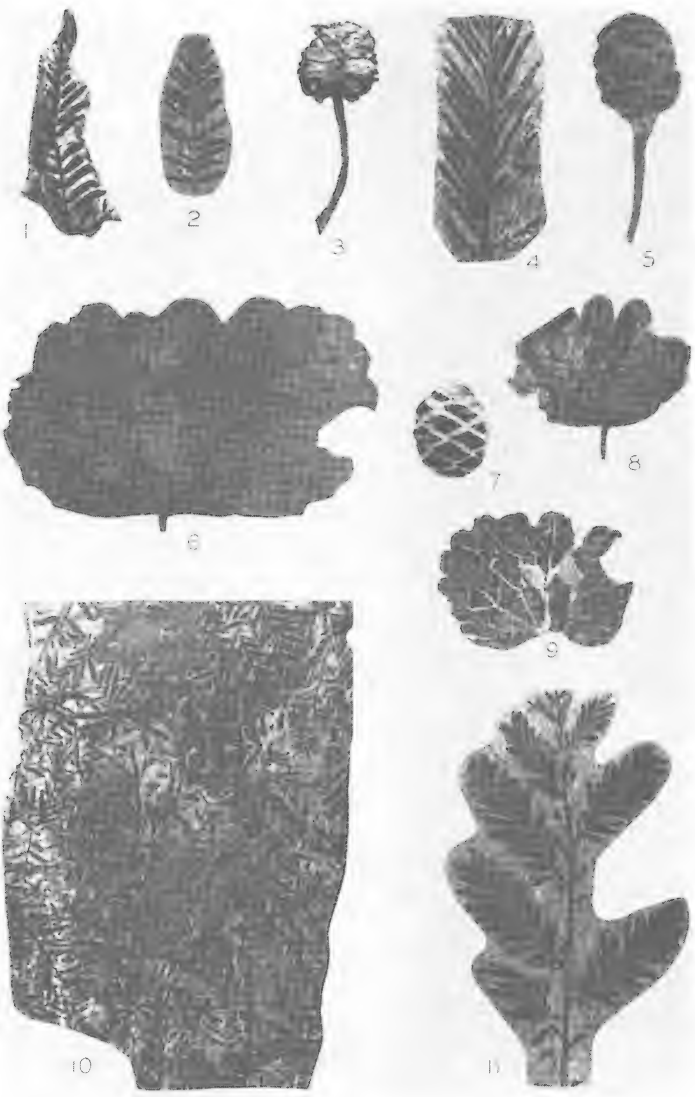

Plate I. Figures 1, 2, 10, 11. *Metasequoia occidentalis* (Newberry) Chaney. Deciduous short shoots. Figures 3, 5, 7. *Metasequoia occidentalis* (Newberry) Chaney. Pistillate cones. Figure 4. *Taxodium dubium* (Sternberg) Heer. Figures 6, 8, 9. *Cercidiphyllum arcticum* (Heer) Brown. All figures approx. X⅓.

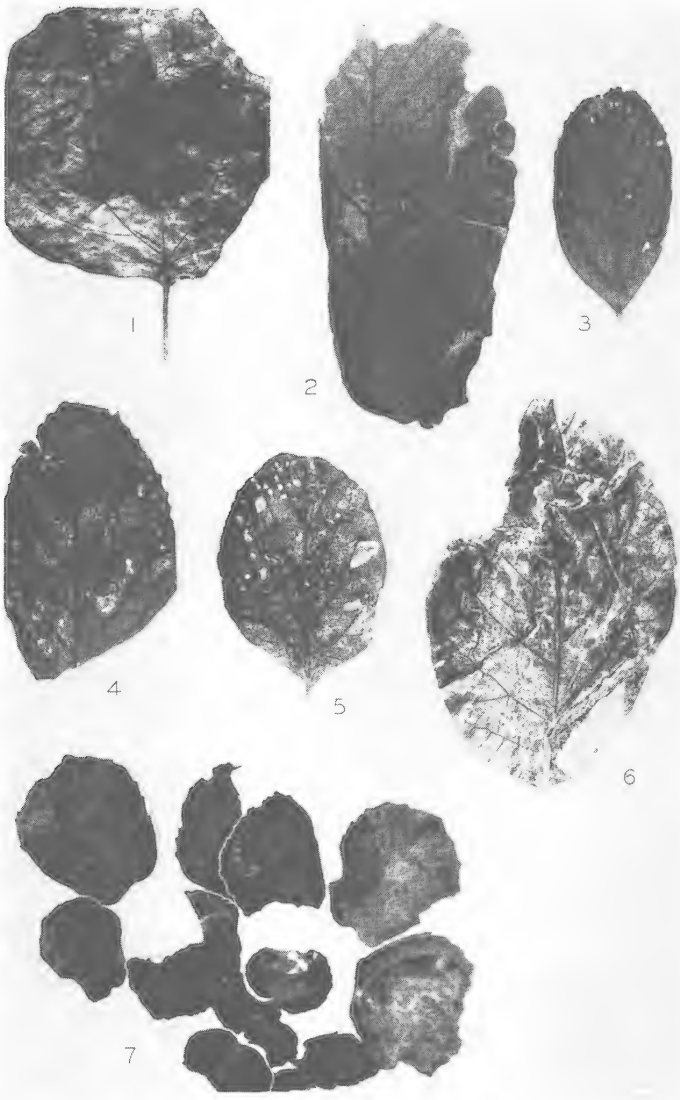

Plate II. Figure 1. *Platanus raynoldsi* Newberry. Approx. X⅓. Figure 2. *Dillenites* sp. cf. *D. ellipticus* Hollick. Approx. X⅔. Figures 3, 4, 5. *Vibernum antiquum* (Newberry) Hollick. Approx. X½. Figure 6. *Pterospermites* sp. cf *P. spectabilis* Heer. Approx. X⅓. Figure 7. *Nymphaeites angulatus* (Newberry) Bell. Approx. X⅓.

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The Sparta Flora from Baker County, Oregon

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THE FOSSIL flora described in this paper is located in the southeast quarter of section 1, T. 7 S., R. 43 EWM, in the southern foothills of the Wallowa Mountains, Baker County, Oregon. It is on the steep slope between Red Knob and Eagle Creek at an elevation of about 4,700 feet and was discovered as a result of logging road construction in 1960. The locality is reached by turning left on a logging road a few hundred feet east of Lily White Guard Station and continuing north and west around the sidehill for about two miles. The locality was reported to me in 1961 by Norman Wagner and Harold Protska, geologists employed by the Oregon Department of Geology and Mineral Industries. Due to the possibility of landsliding and loss of the fossil site thereby, collecting was started immediately and continued until overhanging basalt made further work hazardous. The name Sparta is taken from a mining town eight miles southeast of the fossil locality. Sparta was once a place of some importance but is now practically a ghost town.

The Mascall, Blue Mountain, and Stinking Water floras, of Miocene age, have yielded over 14,000 specimens, which have been identified by Chaney and Axelrod (1959). Chaney (1959) has made these and related floras the subject of intensive study and interpretation, and his work will serve as a standard of comparison in describing other Miocene floras of the region, including the Sparta.

Present Climate and Vegetation

Climatic records were kept from 1928 to 1956 at Cornucopia, elevation 4,700 feet and located 10 miles east of the fossil locality, and from 1891 to 1926 at Sparta, located eight miles southeast near the border of the forested uplands. Precipitation recorded at Cornucopia averaged 44 inches and at Sparta 21 inches. It may be inferred that precipitation at Lily White Station is about 35 inches, much of which occurs as snow. Very little rain falls from July 1 to September 15. Temperature probably ranges from a summer maximum of 95° F to a winter minimum of −35° F.

The following trees and shrubs were noted within two miles of the fossil locality:

Abies grandis
Acer glabrum
Alnus tenuifolia
Amelanchier cusicki
Betula occidentalis
Ceanothus velutinus
Cornus stolonifera
Crataegus douglasii
Larix occidentalis
Mahonia repens
Physocarpus malvaceus
Picea engelmanni
Pinus ponderosa
Populus tremuloides
Populus tricocarpa
Prunus emarginata
Prunus demissa
Pseudotsuga taxifolia
Ribes viscosissimum
Rosa nutkana
Salix scoulerina
Sambucus glauca
Sorbus scopulina
Spiraea lucida
Symphoricarpus albus
Vaccinium membranaceum

It will be noted that the present woody flora is by no means an impoverished one and that it includes plants with a considerable range of ecological requirements. The area is one of decided diversity of habitat, sunny south slopes, shady and steep north slopes, creek bottoms, and a range in elevation of from 3,600 to 5,100 feet.

Of the 24 genera of trees and shrubs growing near the fossil locality today, 12 also grew there in Miocene time: *Abies, Acer, Alnus, Amelanchier, Betula, Mahonia, Picea, Pinus, Populus, Prunus, Pseudotsuga,* and *Salix.* The fossil leaves of *Alnus, Amelanchier, Betula, Picea, Pinus, Populus, Prunus,* and *Pseudotsuga* are very similar to those of species growing in the same area today.

Local Geology

The rocks in the general area of the fossil locality consist of a complex pre-Tertiary group which has been subjected to considerable faulting, folding, and metamorphism, and a much younger Tertiary and later group. The two groups are separated by a profound unconformity. Gilluly (1937), who reported on the geology of the adjacent Baker quadrangle, reached the conclusion that the pre-Tertiary surface "was one of steep hills, if not, indeed, of mountains." The principal unit in the younger rocks is the Columbia River basalt, here a series of flows of olivine basalt with minor tuffaceous interbeds. The Sparta fossil flora was collected from one of these interbeds. Ross (1938) and Protska (1962) have discussed the regional geology and have prepared geological maps of the area.

The Columbia River basalt is thought by Waters (1961:583-611) to be a group rather than a formation, and he has proposed that it be divided

into two distinct formations, the younger Yakima basalt and the older Picture Gorge basalt. The Yakima basalt forms bold rimrocks on erosion, the Picture Gorge basalt a softer profile; the former is poor or lacking in olivine, the latter contains a quite uniform olivine content of 5 or 6 per cent. The basalt at the Sparta locality is of the olivine variety, and is considered to represent the northeastern Oregon equivalent of the Picture Gorge formation. This interpretation is also that of Dr. Harold Protska (1963, personal communication).

Bond (1963) has made a detailed study of the Miocene basalts of the Clearwater area in Idaho, and has separated the Columbia River Group into Lower Basalts and Upper Basalts. He believes that the Lower and Upper Basalts are probably correlative to the Picture Gorge and Yakima formations but that further field work must be done before positive correlation is justified. The Whitebird flora occurs in an interbed in the Lower Basalts and appears to occupy approximately the same stratigraphic position as the Sparta flora.

At the Sparta locality, fossil leaves occur in a soft brown tuffaceous shale; preservation varies from poor to good but averages only fair. The interbed is about 15 feet in width and 5 feet thick, extending an unknown distance into the hillside. Other small interbeds have been uncovered nearby by logging operations; they probably represent ephemeral streams and ponds and may have drained nearby land which had not yet been covered by lava. There is no indication of any interval between flows other than that provided by these small interbeds and chilled zones between individual flows.

Fossil Plant Localities near Keating, Oregon

Extensive tuffaceous lake and stream sediments occur some 8 or 10 miles south and southwest of the Sparta locality. In section 10, T. 8 S., R. 42 E. is a large diatomite deposit which contains numerous but poorly preserved leaf impressions. Gilluly (1937: 62) considered this to be an interbed in the Columbia River lava although the relationship at the diatomite locality was obscure. Protska (1962: 6-7) examined good outcrops of what is apparently an eastward extension of the same deposits and determined that they overlie the basalts. He found no fossils but mentioned vertebrate fossils from similar deposits 12 miles south in the Durkee basin which have been dated as Clarendonian (latest Miocene or earliest Pliocene) by Dr. Arnold Shotwell. The fossil flora mentioned above has been described briefly by Chaney (1959: 64 and 76). He has listed 11 species and has concluded that it was a lowland swamp forest similar to the Mascall flora. In addition to Chaney's list, two

species may be added which were found in beds along the county road about four miles southwest of Keating. The revised list is as follows:

Sequoia affinis
Taxodium dubium
Carya bendirei
Carpinus payettensis
Quercus pseudolyrata
Quercus simulata
Zelkova oregoniana
Magnolia latahensis ?
Liquidambar pachyphyllum
Acer bendirei
Acer glabroides
Nyssa knowltoni
Trapa americana

Comparison of this flora with that at the Sparta locality shows that it contained fewer species and lacked such Asiatic genera as *Ginkgo, Cephalotaxus,* and *Pterocarya;* also that it was a lowland forest whereas the Sparta flora was an upland or slope forest. The reduced number of species, especially of Asiatic forms, is mildly suggestive of a younger age for the Keating flora. However, such local differences in composition may have been simply the result of varied habitats and unrelated to age and floristic development. More will be said about the relative age of the Sparta and other Miocene floras in a later section.

Composition of the Sparta Flora

The Sparta fossil flora consists of leaf impressions, fruits, and pollen. Megafossils and pollen are here listed separately, the first list is of the megafossils, given in the usual systematic order. The first name given is that of the fossil species and its author, the second that of its nearest known living equivalent; the number following is the specimen number given by the Museum of Natural History, University of Oregon, where representative specimens will be kept for reference.

Ginkgoaceae

Ginkgo adiantoides (Unger) Heer—*G. biloba*—4293, 4294.

Taxaceae

Cephalotaxus californica Potbury—*C. fortunei*—4295.

Pinaceae

Abies chaneyi Mason—*A. venusta*—4296.
Picea sonomensis Axelrod—*P. breweriana*—4297.
Pinus harneyana Chaney & Axelrod—*P. ponderosa*—4298.
Pinus wheeleri Cockerell—*P. monticola*—4299.
Pseudotsuga sonomensis Dorf—*P. taxifolia*—4300.

Cupressaceae

Thuja dimorpha (Oliver) Chaney & Axelrod—*T. plicata*—25004.

Typhaceae

Typha lesquereuxi Cockerell—*T. latifolia*—25005.

Monocotyledon of uncertain affinity

Cyperacites sp. Knowlton—possibly a coarse grass—25006.

Salicaceae

Populus payettensis (Knowlton) Axelrod—*P. angustifolia*—25007.
Populus voyana Chaney & Axelrod—*P. tremuloides*—25008.
Salix hesperia (Knowlton) Condit—*S. lasiandra*—25009.
Salix succorensis Chaney & Axelrod—*S. nigra*—25010.

Juglandaceae

Carya bendirei (Lesquereux) Chaney & Axelrod—*C. ovata*—25011.
Juglans browniana Chaney & Axelrod—*J. nigra*—25012.
Pterocarya mixta (Knowlton) Brown—*P. stenoptera*—25013.

Betulaceae

Alnus harneyana Chaney & Axelrod—*A. tenuifolia*—25014.
Betula fairii Knowlton—*B. luminifera*—25015.
Betula thor Knowlton—*B. occidentalis*—25016.
Carpinus payettensis Smith—*C. caroliniana*—25017.

Fagaceae

Quercus dayana Knowlton—*Q. virginiana*—25018, 25019.
Quercus hannabali Dorf—*Q. chrysolepis*—25020, 25021.
Quercus merriami Knowlton—*Q. falcata*—25022, 25023, 25024.
Quercus simulata Knowlton—*Q. myrsinaefolia*—25025, 25026.
Quercus smileyana Chaney & Axelrod—*Q. imbricaria*—25027.

Ulmaceae

Ulmus newberryi Knowlton—*U. americana*—25028, 25029.
Ulmus paucidentata Smith—*U. alata*—25030, 25031.
Zelkova oregoniana (Knowton) Brown—*Z. ulmoides*—25032, 25033.

Nymphaeaceae

Nymphaeites nevadensis (Knowlton) Brown—*Nymphaea* sp.—25034, 25035.

Berberidaceae

Mahonia simplex (Newberry) Arnold—*M. beali*—25036.

Saxifragaceae

Philadelphus pardeei (Knowlton) Brown—*P. lewisii*—25037.

Hamamelidaceae

Liquidambar pachyphyllum Knowlton—*L. styraciflua*—25038.

Platanaceae

Platanus dissecta Lesquereux—*P. racemosa*—25039.

Rosaceae

Amelanchier couleeana (Berry) Brown—*A. sanguinea*—25040.
Prunus chaneyi Condit—*P. virginiana (demissa)*—25041.
Prunus moragensis Axelrod—*P. emarginata*—25042.

Aceraceae

Acer bendirei Lesquereux—*A. saccharinum*—25043, 25044.

Nyssaceae

Nyssa copeana (Lesq.) Chaney & Axelrod—*N. sylvatica*—25045.

Pollen grains were found of the following genera:

Ginkgoaceae
Ginkgo
Pinaceae
Abies
Cedrus
Picea
Pinus
Pseudotsuga ?
Tsuga
Cupressaceae or similar
Genus uncertain
Gnetaceae
Ephedra
Typhaceae
Typha or *Sparganium*
Gramineae
Genera uncertain
Juglandaceae
Carya
Juglans
Pterocarya
Betulaceae
Alnus
Betula
Corylus
Fagaceae
Fagus
Quercus
Ulmaceae
Celtis ?
Ulmus
Hamamelidaceae
Liquidambar
Platanaceae
Platanus
Aceraceae
Acer
Tiliaceae
Tilia
Oleaceae
Fraxinus

Pollen slides were prepared for me by Dr. Alan K. Graham, Harvard Herbarium, and identifications made by Dr. Jane Gray, University of Oregon, and Dr. H. D. MacGinitie, Napa, California. Without their help, the extra information gained as a result of consideration of the fossil pollen would not have been obtained.

Comments on Identifications

In making identifications of megafossils, emphasis was placed on finding their nearest living equivalents; the fossil forms were then considered to be the species given by previous authors as the Miocene equivalents of the nearest similar living species. In most instances, comparisons were made with personally collected living material; where that was not possible, comparisons were made with herbarium and fossil specimens, and with illustrations of Recent and fossil species. I wish to thank Dr. Ralph W. Chaney, Dr. H. D. MacGinitie, and Dr. S. J. Smiley for their help and encouragement, and to absolve them of any responsibility for errors in identification or interpretation.

In addition to the species listed, a number of leaf impressions were found which certainly represent other forms. Some were tentatively identified as

Ceanothus, Cedrela, Crataegus (or *Holodiscus), Fraxinus,* and *Gaultheria.* These were omitted because they were too fragmentary or otherwise poorly preserved to be identified with reasonable certainty.

The presence of *Quercus hannabali* may be questioned, not on account of any paucity of material, but because of the absence of serrate leaves. Otherwise, the leaves fall within the range common to the entire leaves of *Quercus chrysolepis,* considered the modern equivalent of *Quercus hannabali.* The fossil leaves closely resemble those of the northern California huckleberry oak, *Quercus vaccinifolia.*

Quercus merriami and *Q. smileyana* are identified as such because of their close similarity to *Quercus falcata* and *Q. imbricaria,* which are considered by Chaney and Axelrod (1959: 169 and 172) to be their nearest living equivalents. Both fossil species also seem to fall within the leaf limits attributed to *Quercus payettensis,* as now understood (La Motte, 1952: 295). *Q. payettensis* has been compared to the present *Q. morehus,* of California (Smiley, 1963: 216), but the leaves of *Q. morehus* are relatively constant in form, while those of *Q. payettensis,* as illustrated, are quite variable (Knowlton, 1926, as *Q. payettensis, Q. cognatus, Q. rustii,* and *Q. praenigra).* I can find no modern oak with all the leaf forms of *Q. payettensis,* and suspect that Knowlton was correct in thinking that two or more species were present in the Latah flora.

Relative Abundance

The process of fossilization is so highly selective that, in floras such as this where only a few hundred specimens are collected, it is possible to obtain only a general idea of the relative abundance of the plants found. The factors that determine numerical representation have been discussed by many paleobotanists and recently summarized by Chaney (1959: 22-26). Very similar problems apply in the case of pollen counts, an obvious factor being that some plants are wind pollinated while others are not. However, the problem is not entirely hopeless, as it is reasonable to suppose that those plant forms whose fossil remains are found distributed throughout the sediments in some abundance were at least quite common at or near the fossil locality.

The most common megafossils at the Sparta locality are those of *Quercus merriami,* a member of the black (or red) oak group, the live oaks *Q. simulata* and *Q. hannabali,* and *Ginkgo.* Pollen of pine, spruce, elm, and hickory is abundant. In addition, willows, poplars, maples, and sycamores appear to have been at least fairly common.

Paleoecology

It is customary among paleobotanists to consider Miocene plants of the Northwest as being members of East American, East Asian, and Western American elements, according to the distribution of similar living species, and in like manner to divide them into lowland, slope, and montane associations. I do not consider it necessary to go into detail in this respect regarding the Sparta flora as very similar floras have been extensively covered (Chaney, 1959; Smiley, 1963). A study of the Sparta flora reveals that 63 per cent of the forms (pollen genera are also considered) have near relatives in the East American element, 48 per cent in the East Asian, and 54 per cent in the West American. The total adds to over 100 per cent because many forms have similar living equivalents in two or more elements. These percentages are very close to those relating to other Middle to Upper Miocene floras (Chaney, 1959: 130).

Almost all the angiosperms present in the Sparta flora may be assigned without hesitation to a slope association, while the very abundant coniferous pollen suggests a nearby Montane forest. We may assume a small upland valley with a flora of deciduous trees and shrubs, and nearby hills or mountains with a predominately coniferous forest.

In considering climatic conditions at the time of deposition of the Sparta flora, comparison may be made with another slope association flora, the Blue Mountain (Chaney, 1959: 61-88). The principal differences in composition are (1) the most abundant forms in the Blue Mountain flora are *Fagus washoensis, Quercus simulata, Gordonia idahoensis, Sequoia affinis,* and *Crataegus gracilens.* Of these, *Quercus simulata* is common in the Sparta flora, *Fagus* is represented by pollen only, *Crataegus* is doubtfully present, *Gordonia* and *Sequoia* appear to be absent; (2) *Ginkgo* and *Quercus hannabali,* abundant at Sparta, have not been found in the Blue Mountain flora. These differences in floral composition suggest a somewhat higher altitude for the Sparta flora and perhaps a slightly less favorable climate. The flora, taken as a whole, appears to require annual precipitation of 50 or 60 inches, distributed quite uniformly throughout the year, and considerably milder winters than now.

Two plants present problems which cannot be easily resolved as they appear to be completely out of place is a mesic upland flora. One is *Quercus dayana,* whose supposed living equivalent, *Q. virginiana,* is native to the Atlantic coastal plain. Chaney (1959: 57-59) has discussed this problem and has concluded that *Quercus dayana* may have had a wider temperature tolerance than its living equivalent, and also that foliar similarity does not

conclusively establish specific unity. The other misfit is *Ephedra,* an upland desert shrub, the pollen of which is distinctive and therefore probably correctly identified. Martin and Gray (1962: 105) have commented on this problem without finding a very satisfactory explanation.

Age of the Flora

The relative age of various Miocene floras of the Columbia Plateau, based on floristic evidence, has been presented in tabular form by Chaney (1959: 124) and by Smiley (1963: 203). The Sparta flora has most species in common with Chaney's Middle to Upper Miocene group, more specifically with the Mascall, Blue Mountain, Stinking Water, Succor Creek, Trout Creek, Upper Cedarville, and Payette floras. Similarly, it is clearly allied with Smiley's "Vantage to Payette" group (1963, Table 7), also depicted as being of Middle to Upper Miocene age. In addition, it has approximately the same percentage of East American, East Asian, and West American elements as other Middle to Upper Miocene floras.

Reference has been made to the position of the interbed containing the Sparta flora in the "Lower Basalts," thought by Bond (1963: 5-9) to be "probably correlative" with the Picture Gorge basalt, and therefore of pre-Mascall and probably also of pre-Latah age (Waters, 1961: 607). Waters believed the Picture Gorge basalt to be of early or middle Miocene age but added, "We cannot be sure, however, that the basalt that lies unconformably beneath the Yakima basalt in the Imnaha canyon of northeastern Oregon is necessarily the precise age equivalent of that at Picture Gorge." However, this much is clear: both the Picture Gorge basalts and the "Lower Basalts" of northeastern Oregon and adjacent Idaho occupy a stratigraphic position between the Yakima basalts and formations older than the Columbia River basalt group.

How, then, can we explain the apparently younger age assignment based on floristic evidence? A number of possibilities may be mentioned. Floristic differences between the various Miocene floras of the Columbia Plateau may be due more to local environmental conditions than to age relationships. Most of the individual basalt flows apparently followed each other in relatively rapid succession, as suggested by the usual absence of soil zones, so perhaps not enough time elapsed to allow significant floristic changes. The reasoning relative to floristic-age relationship has been stated by Axelrod (1956: 243): "The fundamental principle underlying our interpretations of all Tertiary floras in the far West is that during the period there was a gradual trend toward increased continentality of climate." However, we must

consider the possibility that there was more ebb and flow in the trend toward continentality than generally supposed. If such was the case, close dating of a fossil flora on the assumption of a supposed progressive change could lead to considerable error.

Summing up, a Middle Miocene age is the only determination not in possible conflict with either the floristic or stratigraphic evidence. Without attempting to be so precise, we can safely conclude that the Sparta flora is of Miocene age and neither very early or very late Miocene.

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The Influence of Greasewood on Soil-Moisture Penetration and Soil Chemistry[1]

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THE NATIVE shrubs of desert steppe vegetation are of small size and are widely spaced. This natural arrangement of plants offers opportunities to evaluate the influences of individual plants on their immediate soil environment not possible in more closed kinds of vegetation. Increase of sodium in soil beneath greasewood, *Sarcobatus vermiculatus* (Hook.) Torr., has been previously reported by Fireman and Hayward (1952). Certain nanophyllous Australian shrubs tended to channel precipitation along main stems resulting in increased soil moisture beneath their canopies (Specht, 1957). A circular pattern of pH of surface soil occurred beneath a lodgepole pine canopy with the lowest pH values found near the tree trunk (Zinke, 1962).

This paper presents observations of the influence of greasewood on the depth of soil-moisture penetration and on certain soil-chemical properties, and the pattern of soil-chemical changes as indicated by soil pH.

Methods

Soil samples at 0 to 1 and 1 to 2 dm depths were taken from beneath four greasewood shrubs and from four adjacent intershrub areas with a soil auger. These samples were analyzed for conductivity of saturation extract, cation exchange capacity, and exchangeable sodium and potassium at the soils testing laboratory at Washington State University. The area occupied by the canopies of four shrubs in summer foliage was determined. Entire plants were harvested and the leaves plucked by hand. Leaves were oven-dried at 105° C, reduced to ash, and analyzed quantitatively for major cations with a flame spectrophotometer.

Observations and measurements on the depths of soil-moisture penetrations were made in late January and early February at the time of optimal soil-moisture accretion on the Hanford Reservation, southeastern Washington, in 1963. A soil pit was excavated beneath two greasewood shrubs. Each pit was oriented in an east-to-west direction in such a fashion that one wall

[1] Work performed under Contract No. AT(45-1)-1350 between the Atomic Energy Commission and General Electric Company.

passed through the main stem structure of the shrub and extended beyond the canopy margins. The pits were dug below the depth of moisture penetration so that the front of moisture penetration was readily discernible. Samples collected for pH determinations were taken from the walls of the same pits used to observe moisture penetration. Soil samples were collected from the sides of the pits in a systematic grid pattern beneath the canopy spread and extending beyond the canopy margins and analyzed for pH. The pH of surface samples (0 to 0.5 dm deep) were taken at regular intervals along radii projected from the main stem of each of two additional shrubs. These lines, 9 dm long, extended beyond the canopy margins in eight compass directions. Fresh soil samples wetted with distilled water to paste consistency were used for pH determinations. A battery-operated, glass electrode pH meter graduated in 1/10 pH units was used to obtain readings.

Results and Discussion

A line intercept vegetational analysis of a 30 x 30 meter plot showed that 20 per cent of the ground was occupied by shrub canopies. Greasewood occupied 15 per cent of the ground area, and hopsage, *Grayia spinosa* (Hook.) Moq., 5 per cent. The herbaceous vegetation was comprised largely of grasses. The winter annual cheatgrass, *Bromus tectorum* L., was ubiquitously distributed as a uniform sward with lesser amounts of the small perennial bunchgrass, Sandberg bluegrass, *Poa secunda*, Presl. The depth of moisture penetration in relation to the canopy spread of greasewood shrubs is illustrated in Figure 1. Moisture clearly did not penetrate as deeply under the plant canopy as it did in the region beyond the canopy margins. Moisture penetration was less deep on the eastern side of shrubs where leaf litter also tended to accumulate. Stem-flow was apparently not operable in channeling precipitation along the main stems of the shrubs. Winter precipitation may not be as effective in producing stem-flow as summer precipitation (Specht, 1957). Soil-moisture accretion began in the autumn, and by the first of February only 2.25 inches of precipitation in the form of rain and snow had fallen. Only a trace of rain fell in the entire month of February. Deep moisture penetration in winter is of great importance to plants in this region where the climate is characterized by low annual precipitation (6.73 inches) and hot, dry summers. Deep moisture is relatively free from evaporation losses and is probably exploited less by the shallow-rooted grasses. This moisture can be expected to be stored for use in the spring when air and soil temperatures are more optimal for plant growth.

An approximation of the amount of precipitation intercepted by the leafless canopies of shrubs in winter condition and by accumulations of leaf litter was made by comparing the areas of dry soil and wetted soils beneath

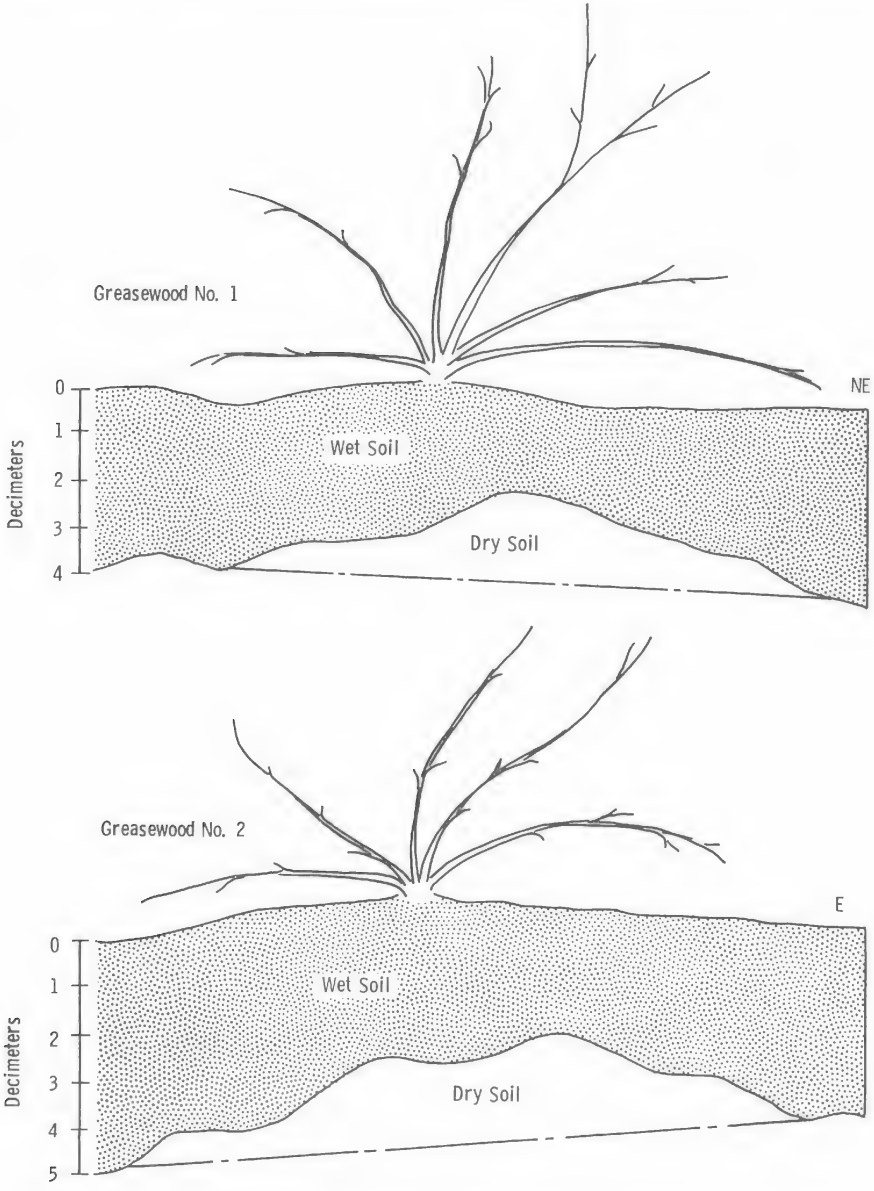

Figure 1. Depth of soil-moisture penetration beneath greasewood canopies.

the canopies as delimited by the depth of moisture penetration beyond the canopy margins (Figure 1). Such a comparison showed that about one-fifth of the precipitation available for soil-moisture replenishment was intercepted by canopy and litter.

The small canopy sizes and wide spacing of shrubs would appear to be of benefit to shrubs by allowing precipitation to penetrate more deeply into the soil in the intershrub areas. However, the factors involved in the persistent maintenance of wide spacing of shrubs are not readily apparent.

The leaves of greasewood accumulated large quantities of sodium (Table 1). The entire leaf crop of four shrubs averaged 232 ± 14 (S.E.) grams of dry leaf per square meter of canopy and yielded 31 grams of mineral cations per square meter of canopy. Of this total 25.5 grams or 82 per cent was sodium.

The soil beneath greasewood canopies reflected the mineral content of the leaves. More exchangeable sodium was measured in the surface decimeter of soil beneath greasewood canopies than in adjacent intershrub areas (Table 2). Similar findings are reported by Fireman and Hayward (1952). Electrical

TABLE 1. The Cation Content of Greasewood Leaves Harvested from Four Shrubs in July, Hanford Reservation, Washington

	mg cation/g dry leaf	g cation/m^2 of shrub canopy/yr
Na	110 ± 5.2	25.5
K	12 ± 2.2	2.8
Ca	10 ± 1.2	2.3
Mg	1.8 ± 0.37	0.42
Total	133.8	31

± Standard error of mean.

TABLE 2. Comparison of Soil Properties beneath Four Greasewood Shrubs and Adjacent Ground, Hanford Reservation, Washington

	Beneath Greasewood		Open Ground	
Depth of soil sample (dm)	0-1	1-2	0-1	1-2
Conductivity mmhos/cm	1.2±0.10	1.7±0.49	0.35±0.041	0.25±0.084
Cation exch. capacity	14 ±1.7	13 ±0.48	13 ±0.48	13 ±0.34
Exch. sodium meq/100 g	7.3±1.3	6.8±0.61	0.082±0.027	0.060±0.024
% Exch. sodium	52	49	0.63	0.46
Exch. potassium meq/100 g	3.5±0.78	2.9±0.92	2.0±0.065	2.4±0.022
% Exch. potassium	25	22	15	18
pH	9.6	9.4	7.6	7.8

± Standard error of mean.

conductivity, pH, and exchangeable potassium were also higher beneath shrub canopies.

Soils with high pH values, i.e., those greater than 8.5, are almost always indicative of high sodium content (U.S. Salinity Laboratory, 1954), and this appears to be an efficient way to detect the distribution of soil sodium in relation to shrub canopy spread. Isopleths of pH of surface soil in relation to canopy spread are shown in Figure 2. The highest pH values, i.e., >9, were restricted to a small circular zone adjacent to the stem. This zone was surrounded by a zone ranging in pH from >8.6 to <9.0. Zones of lesser pH occurred at greater distances from the main stem. Shrub canopies and the zones of high soil pH tended to be skewed toward the east, probably as a result of the strong westerly winds of this region. A similar influence of wind on soil pH is reported by Zinke (1962).

Irregular vertical zonation of pH occurred beneath greasewood canopies (Figure 3). The irregular zonation is probably influenced by the chemical heterogeneity of parent soil material and soil mixing by burrowing rodents as well as by leaching and decomposition of leaf litter. Zones of high pH occurred on the lee side of shrub canopies beneath the region of maximal litter accumulation. It is apparent that greasewood contributes large amounts of sodium to the soil beneath plant canopies. The time required to produce the changes is not known. The usual means of aging woody stems is not applicable to greasewood because it appears to have a discontinuous cambium. However, by assuming that an annual average leaf yield is about 232 grams with an average sodium content of 110 mg/g, it would require only about 16 years to provide 7 meq of exchangeable sodium per 100 g in the upper 1 m^2 x 0.2 m deep volume of soil (bulk density 1.32). Many factors would tend to extend the time required to attain this concentration. One of the most important factors is the effect of strong winds in blowing the leaves far from the vicinity of the shrub canopy. The rates of leaf composition and downward leaching of leaf minerals by precipitation are unknown. The processes involved in placing leaf sodium on the exchange complex of the soil are unknown, but the organic acids in the leaves are believed to play a major role in the exchange reactions (Fireman and Hayward, 1952). It seems reasonable to expect that the soil changes reported in this paper could have occurred within the past 100 years.

Summary

Greasewood shrubs increased exchangeable sodium, potassium, and pH of soil beneath their canopies. The pattern of soil pH corresponded generally

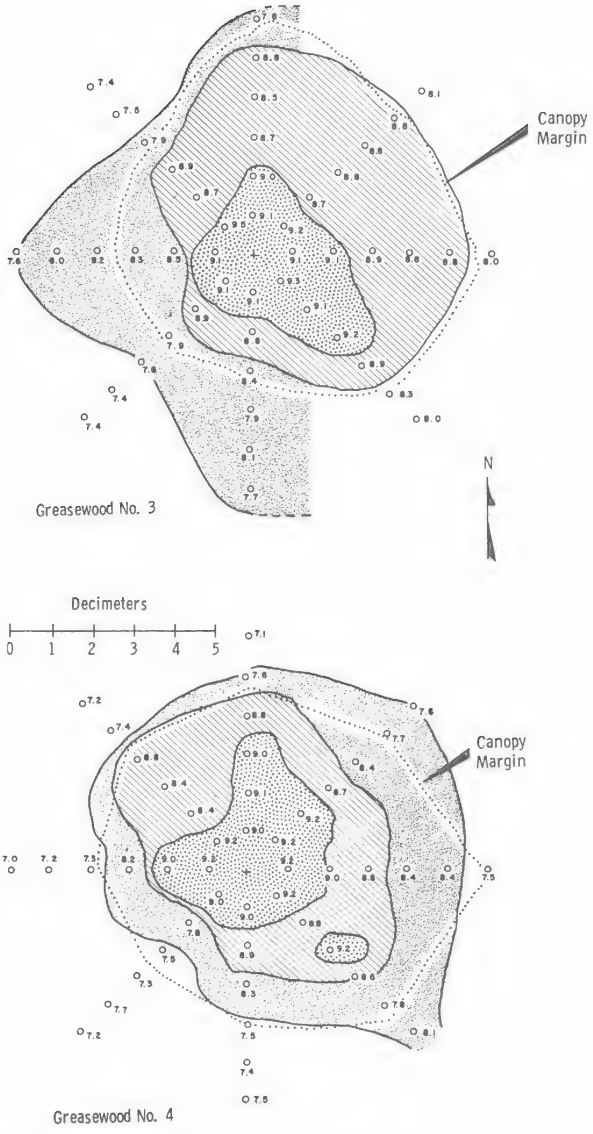

Figure 2. Zonation of pH of surface soil in relation to compass direction and canopy spread of greasewood. Isopleths encompass the following ranges of values: > 9.0 coarse stipple, 8.5 to 8.9 cross-hatch, 7.6 to 8.4 fine stipple, and < 7.5 clear.

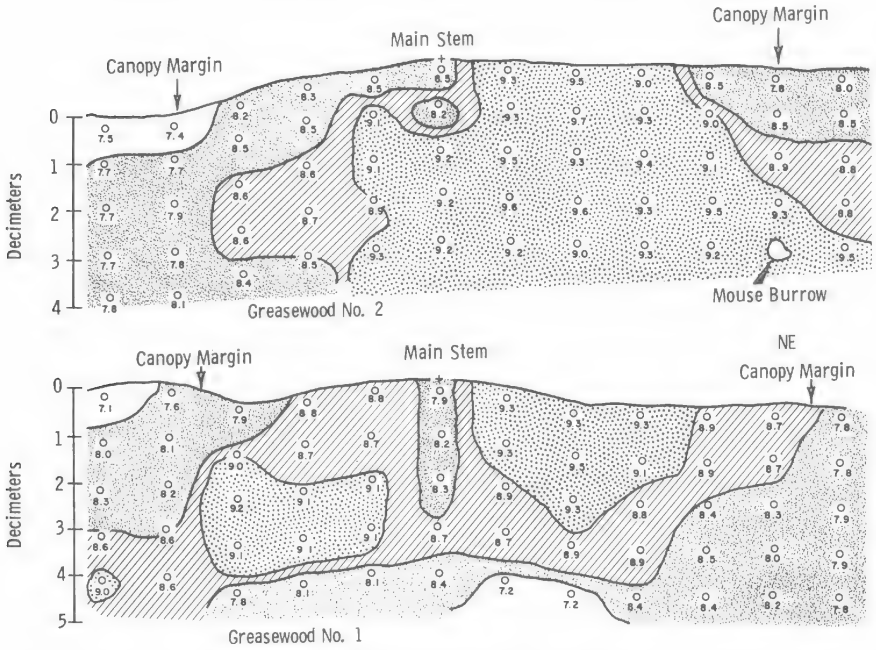

Figure 3. Vertical zonation of pH in soil in relation to canopy spread of greasewood. Isopleths encompass the same values as shown in Figure 2.

to the outline of shrub canopies. The circular pattern of shrub canopy and the pattern of pH were skewed to the east or downwind side of the shrubs. An irregular zonal distribution of pH with soil depth was also observed with maximal pH values confined to the eastern side of the shrubs.

Soil-moisture penetration in winter was less deep beneath shrub canopies than in adjacent intershrub areas. About one-fifth of the moisture available for soil-moisture replenishment was intercepted by shrub canopies and litter. Soil moisture penetrated less deeply on the eastern sides of the shrubs.

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BOOK REVIEWS

Introduction to Animal Parasitology

J. D. Smyth. 1962.
Charles C. Thomas, Springfield, Illinois.
xx + 470 pp., illus. $11.50.

Introduction to Animal Parasitology begins with a discussion of parasitism with special reference to animal associations, i.e., commensalism, phoresis, parasitism, mutualism, and symbiosis. The author recognizes the confusion which exists regarding the term symbiosis but does not take a firm stand on the matter. He stresses the nature of the metabolic relationship between associated species as a criterion in the selection of the term to be applied in each case. The second chapter, "Habitats and Environments of Parasites," emphasizes the physico-chemical conditions of the habitat. Tables are given for oxygen tensions of various organs of different hosts, comparative properties of biles, and other factors of the internal environment. Following this section there are many chapters on the various groups of animal parasites, especially those stressed in most textbooks. But in addition to the usual treatment involving taxonomy, structure, and other matters, the author has added much physiological data. Entire sections deal with the physiology of amoebae, intestinal flagellates, haemoflagellates, and haemosporidia. There are chapters on the physiology of trematodes, cestodes, and nematodes.

Toward the end of the book there are chapters on host reactions against the parasite, immunity to specific parasitic organisms, *in vitro* culture of protozoa, and *in vitro* culture of helminths. The work appeared before it could include the remarkable new *in vitro* culture results of A. Berntzen.

In some instances the author has included sections on parasites mainly of biological interest. Chapters are devoted to the monogenetic trematodes, Aspidogastrea, and "minor" orders of Eucestoda; parts of a number of chapters have interesting discussions of nonhuman parasites.

The 168 figures are pertinent and well executed. There are many original and effective diagrams of life cycles of parasites, and these often include physiological constants of host organs.

The book concludes with an appendix listing common parasites of the laboratory rat and mouse. There is an author and subject-matter index.

This textbook reflects the tendency to upgrade the teaching of parasitology by stressing the physiological viewpoint without abandoning the important traditional material. It ranks among the best of the new texts on the subject.

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Natural History

Richard A. Pimentel. 1963.
Reinhold Publishing Corporation, New York.
xii + 436 pp., illus.

Dr. Pimentel has made a very interesting attempt in this book to introduce the reader to nature study. Although this book is designed as an introduction to the natural sciences, it is in reality an introduction to the natural sciences, as contacted in the field, with particular emphasis on geography, field geology, and field biology. Unfortunately, there is no exposition of the role played by chemistry, physiology, and anatomy in nature.

This book is basically divided into three parts: (a) a discussion of the nonliving world including weather, climate, soils, and geology, (b) a survey of the major taxa of plants and animals, and (c) an introduction to community ecology. The levels of the discussions are not uniform. The exposition of the nonliving world is quite elementary and superficial. On the other hand, the discussions of the living world are extremely detailed. The survey of the

characteristics of the major taxa of plants and animals is very good, although the classification used is not universally accepted. Undoubtedly, the best discussions in the book are those dealing with community ecology and historical biogeography. These are excellent.

The book is illustrated with a wealth of line drawings and diagrams. Some of these illustrations are excellent and clarify the text material to a gratifying extent. At the end of the book Dr. Pimentel has included an extensive and generally quite accurate glossary of the abundance of terms used in the text. At the end of most chapters is a selected bibliography. The value of the book would be greatly increased if these bibliographies included references to publications that would assist in the identification of the number of local faunas and floras.

Natural History by Richard A. Pimentel is an ambitious and pioneering attempt to synthesize a vast body of information needed by the primary and secondary science teacher. It contains much valuable information and discussion; however, it has, as with most pioneering efforts, fallen somewhat short of its goal. It is anticipated that a revised edition will be of great value to the introductory science teacher.

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Invertebrate Zoology

Robert D. Barnes. 1963.
W. B. Saunders Company, New York.
632 pp.

Invertebrate Zoology is certainly a sincere attempt by the author to approach, for the United States, a volume of similar quality to that of the near-classic work on invertebrates by Borradaile, Eastham, Potts, and Saunders. The author has relied heavily on the work of Libbie Hyman and her associates in the formulation of materials and format. He has departed from the classic approach by treating most phyla in a general way as contrasted with the "type animal" approach. Much may be said in support of either view. Most of our students, however, have indicated a preference for the author's treatment.

Some of our student criticisms might well be taken into account in an evaluation of this text. An outline of invertebrate classification has been indicated as desirable. Much comment about the quality of drawings was made, with the view that these were too diagrammatic, lacking detail of internal structure, and incompletely labelled. The group, as a whole, suggested that more photographs be included in the text. Reference material was judged difficult to find, and in this sense the text does not fill the need of graduate students. It should be better indexed. The students felt in general that the author tends to wander around a certain subject matter, and that a more concise treatment would be more desirable. Some students felt the need for a glossary of terms—a most useful item for the undergraduate student. It was also suggested that the systematic resumé of each group be taken to Family instead of to Order. The students also pointed out that the dye rubs off the cover. Very little physiology, apart from that directly related to the existence of the animal, is included.

In spite of these shortcomings, this reviewer would commend the text for a good, general course in invertebrate zoology.

Philip A. Buscemi
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Biochemistry: An Introduction

P. H. Jellinck. 1963.
Holt, Rinehart and Winston, New York.
308 pp. $6.00.

The author, an associate professor of biochemistry at the University of British Columbia, has written this book at an elementary level for students who do not intend to specialize in biochemistry and who have a limited background in chemistry and biology. A further objective is "to convey to the reader the scope and dynamic nature of biochemistry."

To achieve his purpose, the author has divided the book into 12 chapters. The first two chapters are concerned with the structure and chemistry of the cell and with metabolism and methods used in metabolic studies. The next eight chapters cover the chemistry and metabolism of carbohydrates, lipids, proteins, and nucleic acids. The final chapters deal with the vitamins and hormones. The bibliography consists of three standard textbooks and 12 additional review articles or books on specialized topics. A 14-page index is provided.

Because of the intended audience and the length of the book, explanations are descriptive rather than analytical. The emphasis is on animal and particularly human biochemistry. Discussions are necessarily brief, and details are lacking. A number of useful figures and illustrations are included. While many structural formulas are given, the author states, "they need not be memorized and should not deter the average student."

While the book will be of interest to persons wishing to know something of the nature of biochemistry, this reviewer believes a cheaper paperback volume would find wider usage.

Duane Le Tourneau
University of Idaho

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Phenotypic Variation and Repeatability of Stem Sinuosity in Douglas-fir

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SINUOSITY IS one of the more conspicuous stem-form defects in young Douglas-fir. As defined here, sinuosity is any stem crookedness or displacement from the vertical that is confined within an interwhorl stem segment. It should not be confused with major stem contortions, such as sweep or corkscrew growth, whose effects are continuous throughout several interwhorls.

Sinuosity is an important cause of compression wood, since any slight dislocation of the leader from the vertical brings about formation of compression wood below the dislocation (Burns, 1920; Mergen, 1958). Minor stem crooks are covered by eccentric wood growth after a few growing seasons, leaving an outwardly normal-appearing stem with a central core containing compression wood.

Compression wood has inferior properties for lumber and pulp due to its shorter fibers, greater fibril angle, and high lignin content (Dadswell and Hawley, 1929; Wardrop and Dadswell, 1950). Pound for pound it is weaker than normal wood; it is a major cause of bowing and twisting during kiln drying; it is abnormally hard in lumber; and it is undesirable in veneer in which strength and neatness are important (Brown *et al.,* 1949). Sulfate pulps made from compression wood are somewhat inferior and sulfite pulps are greatly inferior to pulp made from normal wood (Watson and Dadswell, 1957). Curran (1936) reported that pulp from compression wood was 10 per cent lower in yield and 60 per cent lower in strength properties than pulp made from normal wood.

The quantity of compression wood in a stem is likely to be directly related to its degree of sinuosity. Zobel and Haught (1962) reported that in loblolly pine, 9-17 years old, compression wood ranged from 6 per cent of the merchantable volume in straight-stemmed trees to 16 per cent in those with considerable stem corkscrew. The stem of one excessively crooked tree contained 67 per cent compression wood.

Corkscrew stem has been demonstrated to be strongly inherited in slash pine (Mergen, 1955) and in loblolly pine (Perry, 1960), and Haught (1957) has suggested that compression wood may be decreased in future stands by breeding trees with less crook or spiral. The possibility that stem sinuosity might also be strongly inherited prompted the present study.

This paper reports results of a preliminary study of variation and inheritance of stem sinuosity in Douglas-fir, made to determine the feasibility of upgrading future stands by choosing parents from the straight trees in natural stands or in seed-production areas. Tree-to-tree variation was examined in trees 10 to 20 years old in 15 stands located in three Weyerhaeuser tree farms in southwestern Washington. Repeatability values are computed from data for 60 trees in two stands to estimate the upper limit of stem-sinuosity heritability. Correlations between sinuosity and other stem or stand characteristics are also examined.

Materials and Methods

The first problem was to develop an objective scoring method for distinguishing degree of sinuosity. A particular score should represent a given degree of crookedness, or displacement of the stem from vertical, whatever the size or condition of the tree. A score which satisfied these requirements was obtained by using the transformed secant of angle z of a right triangle (Figure 1A). The secant is obtained by computing h/a where a equals vertical length of the interwhorl and h equals length along the sinuous stem (Figure 1B); the transformation is (secant value − 1) x 100. This score

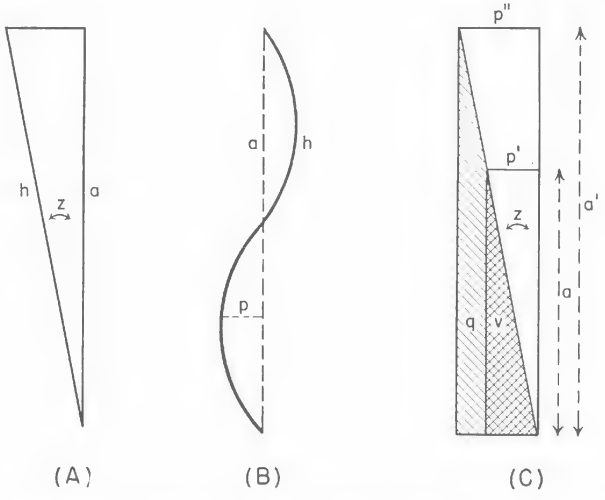

Figure 1. Diagrammatic representation of method used for scoring stem sinuosity.

measures sinuosity in one plane. A second reading is also required in a plane at 90 degrees from the first. Total score for an interwhorl stem segment is the sum of scores for the two planes.

This method of scoring has a disadvantage in that a given score may not represent similar volumes of compression wood over different interwhorl stem lengths (Figure 1C). Consider two stem interwhorls with lengths (a) and (a') but with identical scores, i.e., identical angles of z. Amplitude of departure of the sinuous stem from vertical is p (Figure 1B), and the analogous diagrammatic measurement for the short stem in Figure 1C is p' and for the long stem p''. Compression wood forms below any inclined portion of a stem, and, therefore, compression-wood volume in a stem will likely be related to volume of wood below a stem curve. Thus, compression-wood volume in a short interwhorl a will be approximated by area v in Figure 1C, in contrast to the larger area $q + v$ for the longer interwhorl a'. Therefore, two trees that have similar degrees of sinuosity may not produce similar volumes of compression wood.

Thirty trees from each of 15 areas in three tree farms were rated for sinuosity of the second interwhorl from the tree top, and measured for total height and age above breast height. The tree farms are located in a triangle with sides of 40, 50, and 80 miles in southwestern Washington. Extreme outermost boundaries of the five areas in each tree farm were separated by as much as 15 miles. For each area, every undamaged, relatively open-grown tree was measured along a given roadside until 30 trees had been rated. For each tree, the second interwhorl was examined visually and scored for sinuosity in two vertical planes at right angles.

For 60 trees in two areas, first and second interwhorls were photographed in two planes at right angles. To provide a common scale for length and diameter measurements and vertical orientation, a plumb, graduated rule was photographed in every exposure (Figure 2). Vertical stem length and length along the stem were measured for each interwhorl with a Dietzgen wheel-type map ruler from tracings of the projected photographs. Duplicate measurements were required for sufficient accuracy. First and second interwhorls for each of the 60 photographed trees were scored from the resulting data. Stem diameter immediately above the first whorl was also determined.

The visual system for rating sinuosity was evaluated by comparing measured scores with rated scores for second interwhorls of trees in the two photographed areas. Correlation coefficients between the 30 pairs of observations in each of the two areas were found not to be significantly different and were combined, after the manner of Snedecor (1956: 179), to give $r = 0.76^{**}$.

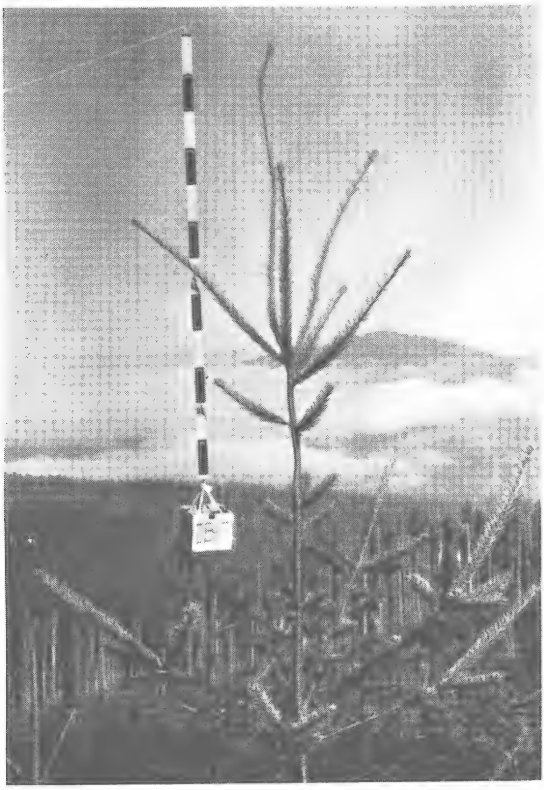

Figure 2. First and second stem interwhorls of Douglas-fir with plumb rule graduated in decimeters (3.94 inches).

From this the rating system was judged sufficiently accurate for purposes of this study. The regression equation, $Y = 1.5597 + 0.2424X$, common to both areas, was used to compute measured scores from rated scores. Here, Y = measured total score for sinuosity in two planes and X = the corresponding total rated score.

Results

Frequency distributions for total sinuosity scores of photographed trees illustrate several general trends (Figure 3). For all areas, scores are skewed toward the higher values, and skewness is more pronounced for scores in interwhorl 1 than in interwhorl 2. Also, the average degree of sinuosity is greater above whorl 1 than between whorls 1 and 2. These latter conditions undoubtedly result from stem straightening and from "filling in" of a portion of the stem crooks in the second interwhorl by eccentric wood formation.

TABLE 1. Frequency and Degree of Stem Sinuosity for Interwhorl 2 of 30 Trees in Each of 15 Study Areas, with a Summary of Average Area Age, Height Increment and Elevation

Tree farm	Area No.	Elevation (feet)	Mean age above b.h. (yrs.)	Mean annual height increment above b.h. (ft/yr)	Frequency of sinuous interwhorls		Degree of sinuosity	
					Per cent straight—measured[a] score < 2	Per cent strongly sinuous—measured[a] score > 5	Mean measured sinuosity	Mean rated sinuosity
Clemons	1	1,500	9.3	2.46	23	3		5.6
	2	800	10.6	2.79	17	0		5.2
	3	690	6.7	2.61	50	7		3.7
	4	600	10.4	2.98	37	7		4.2
	5	600	8.8	2.69	27	7		5.1
Average		838	9.2	2.71	31	4.7		4.8
St. Helens	1	1,500	10.7	2.58	43	0		3.9
	2	2,200	12.1	2.06	17	0		4.5
	3	2,350	12.7	1.98	33	0		3.6
	4	2,850	9.5	2.28	23	3		3.7
	5	2,950	10.1	2.08	20	3	3.4	5.2
Average		2,370	11.0	2.20	27	1.3		4.2
Vail	1	2,000	10.3	2.11	23	3		5.3
	2	1,920	12.0	2.42	30	7		4.9
	3	2,400	12.2	2.08	37	3		3.9
	4	1,500	7.4	2.66	40	7	2.0	4.4
	5	2,400	9.3	1.77	50	0		3.3
Average		2,040	10.2	2.21	36	4.0		4.4
Average all areas		1,750	10.1	2.37	31	3.3		4.4

[a] Measured score computed from rated score by regression.

Figure 3. Distribution of total sinuosity scores for 60 measured trees in two areas.

Variation in sinuosity among areas is summarized in Table 1, along with stand information, including age of trees above breast height, average height growth per year, and area elevations. Variation data pertain only to sinuosity of the second interwhorl. Differences in mean sinuosity among tree farms are not significant, whereas differences among areas within tree farms are highly significant (Table 2). The common standard deviation in measured

TABLE 2. ANALYSIS OF VARIANCE IN AVERAGE TOTAL SINUOSITY (ARCSIN TRANSFORMATION) AMONG AREAS WITHIN TREE FARMS

Source of variation	*d.f.*	*Mean squares*	*Significance*
Total	448		
Tree farms	2	80.84	Nonsignificant
Areas within farms	4	212.65	Significant at 1 per cent level
Individuals within areas	442	41.00	

sinuosity for the two photographed areas is 1.16; the average sinuosity is 2.75, and the resulting coefficient of variation is 42 per cent.

An alternative method for examining sinuosity variation is to compare frequencies of straight versus strongly sinuous interwhorls within areas. For

frequency data in Table 1, an interwhorl was considered straight if its measured score was less than 2, and strongly sinuous if its score was greater than 5. As an example, in Figure 1B, the sinuous line *h* represents a score of 5. Areas do not differ significantly in the frequency of either straight or strongly sinuous second interwhorls. The data also indicate that in any given growing season, 10 straight interwhorls are produced for every strongly sinuous one. Furthermore, approximately 65 per cent of the interwhorls produced in that growing season are moderately sinuous, i.e., they have a score greater than 2 and less than 5.

A second objective of the study was to estimate heritability of stem sinuosity. Unfortunately, heritability cannot be obtained directly in a wild population where hereditary relationships between trees are not known. Upper limits of heritability, however, can be estimated by calculation of repeatability (Falconer, 1961) for traits which may have several discrete production records in the lifetime of an organism. In Douglas-fir stem sinuosity has the opportunity to show itself in the stem leader produced each growing season and is, therefore, such a trait. To measure repeatability, intraclass correlation was calculated between sinuosity in the first and second interwhorls of the 60 trees in the two photographed areas. Coefficients were small and statistically nonsignificant: for St. Helens (Area 5), $r_1 = .144$; for Vail (Area 4), $r_1 = .176$. When the coefficients were combined into a single estimate of intraclass correlation, the combined $r_1 = .176$ with 0.99 confidence limits on r being $-.17$ to .48.

In the Douglas-fir region sinuosity is commonly thought to be "caused" by conditions that produce extraordinarily long leaders as a result of exceptionally rapid height growth or of an extended period of height growth. Three corollary hypotheses follow: (1) Sinuous trees are more frequent on highly productive sites. (2) The average degree of sinuousity is greater on highly productive sites. (3) Age of a tree affects sinuosity through the influence of age on height growth. Another common speculation is that sinuosity is more prevalent in trees with exceptionally slender leaders. This study provides an opportunity for examining these hypotheses.

Simple correlation coefficients of rated sinuosity with age of trees at breast height and with mean annual height increment above breast height were computed for every area (Table 3). Coefficients for either were not found to be significantly different among all areas. The 15 coefficients for each comparison were then combined into single estimates of correlation (Snedecor, 1956: 178). The resulting combined correlation coefficients are $r = 0.157$ between sinuosity and age, and $r = 0.163$ between sinuosity and

TABLE 3. CORRELATION OF TOTAL RATED SINUOSITY (ARCSIN TRANSFORMATION) WITH TREE AGE AND ANNUAL HEIGHT INCREMENT FOR 30 TREES WITHIN EACH OF 15 AREAS

Tree farm	*Area*	*Correlation coefficients of sinuosity with*	
		Age of Tree at b.h.	*Mean annual height increment above b.h.*
Clemons	1	.19	–.04
	2	.20	–.04
	3	.23	.49**
	4	.24	.28
	5	.02	.04
St. Helens	1	.46**	.16
	2	.03	–.27
	3	.23	.34
	4	.21	.26
	5	.13	.06
Vail	1	.06	.07
	2	.25	–.15
	3	.14	.37*
	4	.30	.47**
	5	.01	.26

*Significant at 95 per cent level.
**Significant at 99 per cent level.

mean annual height increment. Both coefficients are statistically highly significant, but, in either case, the degree of association is so slight as to make the correlations almost meaningless in a practical or biological sense. Variation in sinuosity is associated with only 2.5 per cent of the variation in age ($r^2 = .025$), and with 3 per cent of the variation in mean annual height increment ($r^2 = .027$). Furthermore, data in Table 1 indicate no significant relationship between average sinuosity in a stand and mean stand age, or between average sinuosity and mean annual height increment for the stand.

The conjecture that excessive leader length and less-than-average stem diameter cause stem sinuosity in Douglas-fir can also be examined by path correlation analysis (Wright, 1921, 1922). This method is suitable for investigating the logical consequence of such a hyphothesis, but validity of results from the method hinges on a priori knowledge of cause-and-effect relationships among variables. Dewey and Lu (1959) give an excellent account of the arithmetic mechanics necessary for the analysis; Wright (1922) clearly explains the theory, restrictions, and pitfalls of the method. Path

correlation coefficients are a type of standardized partial regression coefficient and provide estimates of the direct influence of one variable upon another in a given causal scheme. They are calculated from correlation coefficients used in conjunction with a path diagram. The path diagram denotes causal relations in the system being investigated.

TABLE 4. CORRELATIONS AMONG MEASURED TOTAL SINUOSITY (ARCSIN TRANSFORMATION), LENGTH[a] AND DIAMETER OF LEADERS FOR 30 TREES IN EACH OF TWO AREAS[b]

	Diameter at base of leader	*Sinuosity of leader*
Diameter at base of leader		.521**
Length of leader	.771**	–.004 N.S.
	.562**	.137 N.S.

[a] Length was measured along the sinuous stem, e.g., the length of *h* in Figure 1B.
[b] Coefficient for St. Helens Tree Farm above, Vail below, in each box. Vail coefficient corrected for attenuation because of considerable measurement error.
*Significant at 95 per cent level.
**Significant at 99 per cent level.

Based on the path diagram in Figure 4, path coefficients were calculated for each of the two photographed areas from correlation coefficients in Table 4. Reliability of the absolute values of path coefficients is questionable since the set of coefficients for each area is based upon 30 observations only (Table 5). However, four definite trends appear when coefficients for the two areas are compared: (1) Longer leaders are directly associated with less sinuosity ($P_{13} = -1.00, -.15$). (2) Larger leader diameters are directly associated with more sinuosity ($P_{23} = 1.29, .51$). (3) The association between diameter and sinuosity is considerably greater than between length and sinuosity (compare absolute values of P_{13} with P_{23}). (4) A considerable portion of

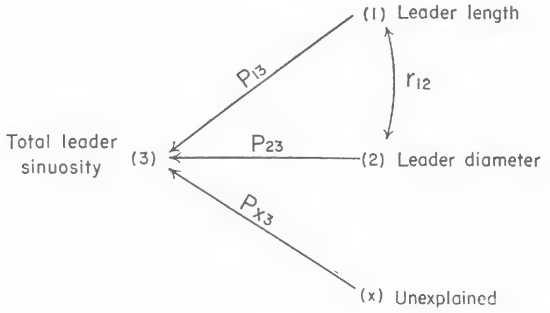

Figure 4. Model for path coefficient analysis.

TABLE 5. RESULTS OF PATH ANALYSIS OF RELATIONSHIPS AMONG LEADER SINUOSITY, LENGTH AND DIAMETER OF 30 TREES IN EACH OF TWO AREAS

	Path correlation coefficients, a measure of the direct effect of		
Area	*Leader length on sinuosity* (P_{1x})	*Leader diameter on sinuosity* (P_{2x})	*Unexplained, including error, on sinuosity* (P_{ex})
St. Helens – 5	–1.00	1.29	.57
Vail – 4	– .15	.51	.90

the variation in sinuosity is not directly associated with length or diameter of the leader (compare $P_{ex} = .57, .90$ with absolute value of P_{1x}, P_{2x}). The above trends directly contradict the commonly accepted hypothesis that long, slender leaders are most sinuous.

Discussion and Conclusions

The practical objective of this study was to determine whether or not stem sinuosity in succeeding rotations could be decreased appreciably by collecting seed from straight trees in existing stands or in seed-production areas rogued of sinuous trees. In either case, mass selection is the breeding method being practiced, and the amount of improvement depends on trait variation, trait heritability and selection intensity. Variation in sinuosity is more than adequate for rapid genetic improvement. Within-population variation is high (coefficient of variation = 42 per cent), and significant between-stand differences provide an added source of variation. The evidence concerning heritability is less conclusive. Lack of knowledge about hereditary relationships between trees required that repeatability be used as a measure of the upper limit of heritability. The resulting repeatability value, $r_1 = .176$, is not statistically significant. Nevertheless, at present, it provides the best available basis for estimating sinuosity heritability in wild stands of Douglas-fir. Since repeatability is likely to be two or three times greater than narrow-sense heritability under forest conditions (Campbell, 1961), heritability of sinuosity is probably less than 10 per cent.

The selection intensity obtained in seed-production areas or by collecting cones from less sinuous trees in wild stands will undoubtedly also be small. No more than 50 to 70 per cent of trees in the original stand are usually rogued from a Douglas-fir seed-production area. These levels of roguing provide theoretical selection intensities of 0.8 and 1.16, respectively (Lerner,

1958: 114). It is unlikely that greater selection intensities will result from selective cone-collection practices in wild stands.

For the above conditions, calculation of genetic response from mass selection predicts a 4.9 per cent gain toward stem straightness per breeding generation. The prediction is based on heritability of 10 per cent, selection intensity of 1.16, and a coefficient of variation of 42 per cent. The equation used in prediction also assumes a statistically normal distribution of the trait in the population. Distribution of sinuosity, on the contrary, is strongly skewed away from straight-stemmed trees. This causes selection intensity and within-population variation to be considerably overestimated. Genetic gain will, therefore, be less than predicted, probably about 2 to 4 per cent.

Mass selection is inefficient for traits with low heritability and especially so where conditions prohibit high selection intensities. Under the circumstances, one or the other of the several forms of family or within-family selection is more effective (Falconer, 1961). These methods imply an intensive breeding program, which may or may not be economically justified for stem sinuosity in Douglas-fir. The effect of sinuosity on utilization of wood from young trees has not yet been evaluated. Until this is done, and until the probable range of stem-sinuosity heritabilities is more precisely determined, the trait should not be included in the selection index for an intensive breeding program.

A path analysis was used to evaluate the hypothesis that long slender leaders are more sinuous. It should be emphasized that a path coefficient measures the influence of one variable on another from a particular viewpoint—in this case, the cause and effect relationship shown in Figure 3. It is unlikely that leader length of diameter "causes" sinuosity in the strict sense implied by the path diagram; it is more likely that leader length and diameter react to sinuosity. Stem movements caused by wind stimulate the cambium to produce greater diameter growth (Jacobs, 1954), and stem lean also causes eccentric diameter growth and the formation of compression wood. By analogy, the greater diameter at the base of sinuous leaders may result from diameter growth to compensate for stresses caused by out-of-vertical orientation of the leader. Furthermore, tissue adding diameter to a stem may compete more favorably for carbohydrates, nutrients, or water than does elongating tissue, resulting in less total elongation of the sinuous stem.

Summary

A preliminary study of variation and inheritance of sinuosity (any stem crookedness or displacement from the vertical that is confined within an interwhorl stem segment) was made to determine feasibility of upgrading

future Douglas-fir stands by collecting seed from straight trees in natural stands or in seed-production areas. Results are based on measurements made in 30 Douglas-fir trees, 10 to 20 years old, from each of 15 areas in three Weyerhaeuser tree farms. Differences in mean sinuosity among areas within tree farms are highly significant, whereas, differences among tree farms are not. Within-area tree-to-tree variation is high (CV = 42 per cent). Heritability is probably less than 10 per cent based on a study of repeatability in first and second interwhorls. A 2 to 4 per cent genetic improvement toward straight-stemmed trees is tentatively predicted for seed collected in carefully rogued seed-production areas.

A path-coefficient analysis indicates that, within a given area, short leaders with larger diameters are more likely to be highly sinuous than long, slender leaders.

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The Vegetation of Montana—A Bibliography

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A COMPREHENSIVE listing of the known references to the vegetation of Montana is provided here to complement other recently published bibliographies for other Pacific Northwest states. The earliest descriptions and references to the Montana vegetation included in this bibliography are those concerned with the analysis and tabulation of plants collected during the Lewis and Clark expedition (Pursh, 1814; Meehan, 1898). Later botanical expeditions into Montana occurred frequently just prior to and during the last half of the nineteenth century (Hooker, 1847; Gray, 1860; Porter, 1872; Coulter, 1873; Chickering, 1878; Lieberg, 1884; Newberry, 1884; Seymour, 1889; Carleton, 1893; and several others).

Several authors listed in this bibliography have made outstanding contributions to our knowledge of the Montana vegetation. These include P. A. Rydberg, whose taxonomic and phytogeographical studies throughout the Rocky Mountains supplied one of the first detailed descriptions of the flora of this region; J. W. Blankinship, pioneer professor of botany at Montana State College, whose efforts were directed to the development of a specific flora of Montana; and J. E. Kirkwood, early professor of botany at Montana State University, whose detailed ecological descriptions and interpretations of the forest communities in Montana provided a foundation for forest management in this area.

Contributions to this bibliography of Montana vegetation appear in a great number of contemporary, professional scientific periodicals. It is noteworthy to point out that significant information is also available in unpublished graduate theses prepared by students at Montana State University and Montana State College. Although less easily available for reference, these theses are considered of sufficient importance that pertinent titles are listed in this bibliography.

All significant references to the vegetation of Glacier National Park are also provided. Excepted, however, are the numerous brief notes to the plants and forests of Glacier Park which occur in the discontinued, mimeographed publication, *Glacial Drift.*

Other references purposely omitted in this bibliography are those that mention or discuss Montana vegetation in very general terms as a part of broad regional studies.

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Plant Communities of Oregon: A Bibliography

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THIS BIBLIOGRAPHY is a listing of references containing information on plant communities of Oregon. Only those references which provide information on composition, ecology, or distribution of communities are included: references limited to the autecology of individual species are not included. Because so much useful information on Oregon plant communities is found in unpublished theses, we have included those which have come to our attention.

Synecological studies conducted in Washington, Idaho, British Columbia, and California are often relevant. Bibliographies on plant communities in three of these areas are also available and should be consulted.[1]

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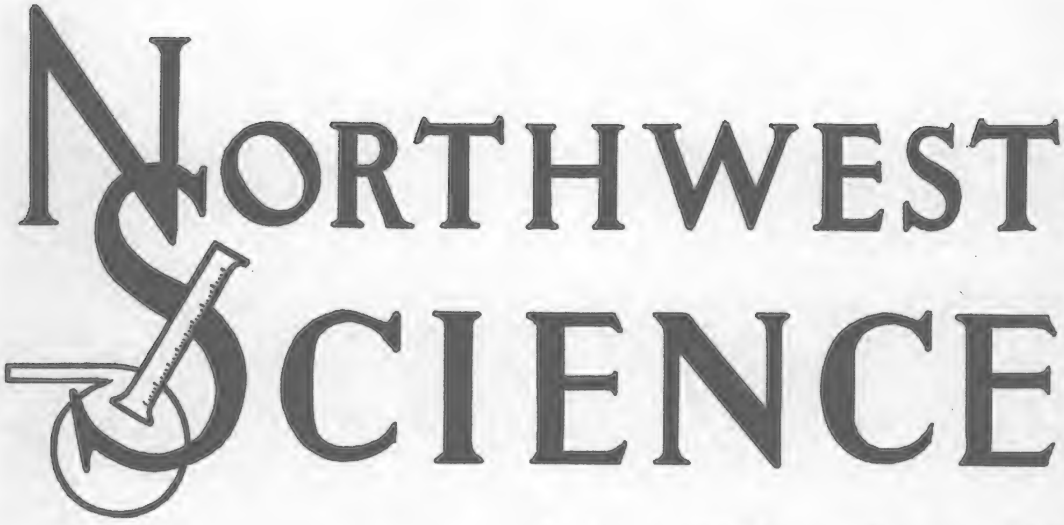

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The Carbonate Content of Surface Sediments from the Northeast Pacific Ocean[1]

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THE DEEP ocean sediments of the North Pacific Ocean differ in many respects from those of the South Pacific Ocean (Sverdrup and others, 1942; Bramlette, 1961); variations in the carbonate contents are especially pronounced. For example, calcareous oozes are common in the South Pacific but rare in the North Pacific. Revelle and others (1955) suggested that variations between the deep ocean sediments of the Atlantic and Pacific Oceans were caused by regional differences in river runoff and sediment discharge in the ocean.

Such effects on a smaller scale are evident near the North American coast between Cape Flattery, Washington, and Cape Mendocino, California (Nayudu, 1959), an area where the Columbia River as well as numerous smaller coastal rivers discharge into the North Pacific Ocean (Figure 1). The carbonate content of 95 modern marine sediments from this area was determined as part of a study of the relative rate of deposition of calcareous biogenous constituents (foraminifera, coccolithophores, etc.) as compared with the deposition rate of noncalcareous or low-carbonate sediment, largely derived from the land.

Nayudu (1959), Enbysk (1960), and Nayudu and Enbysk (in press) studied the relative abundances of calcareous and siliceous biogenous constituents as well as the lithogenous constituents in the coarse fraction (>62 microns) of the sediment from the Northeast Pacific Ocean. They described seven "bio-lithologic areas" in the Northeastern Pacific Ocean and discussed the influence of the ocean circulation and bottom topography on the accumulation of marine sediments in the region.

McManus (1964) reviewed the literature, discussed nomenclature of the physiographic features of the same area and concluded that at least three physiographic provinces can be distinguished: (1) the continental terrace, (Continental Shelf and Continental Slope), (2) Cascadia Basin, and (3) "a province of irregular topography on the western flank of the basin." For

[1] Contribution No. 343 of the Department of Oceanography, University of Washington.

this study, I have further divided Cascadia Basin into Eastern Cascadia Basin and Western Cascadia Basin, with Vancouver Valley and the southern portion of Cascadia Seachannel as the dividing line (Figure 1). Tufts Plain and the Seamount Provinces are delineated approximately as shown by Hurley (1964). More detailed analysis of the bottom topography in this region may require significant changes in the preliminary delineations of the physiographic provinces used here.

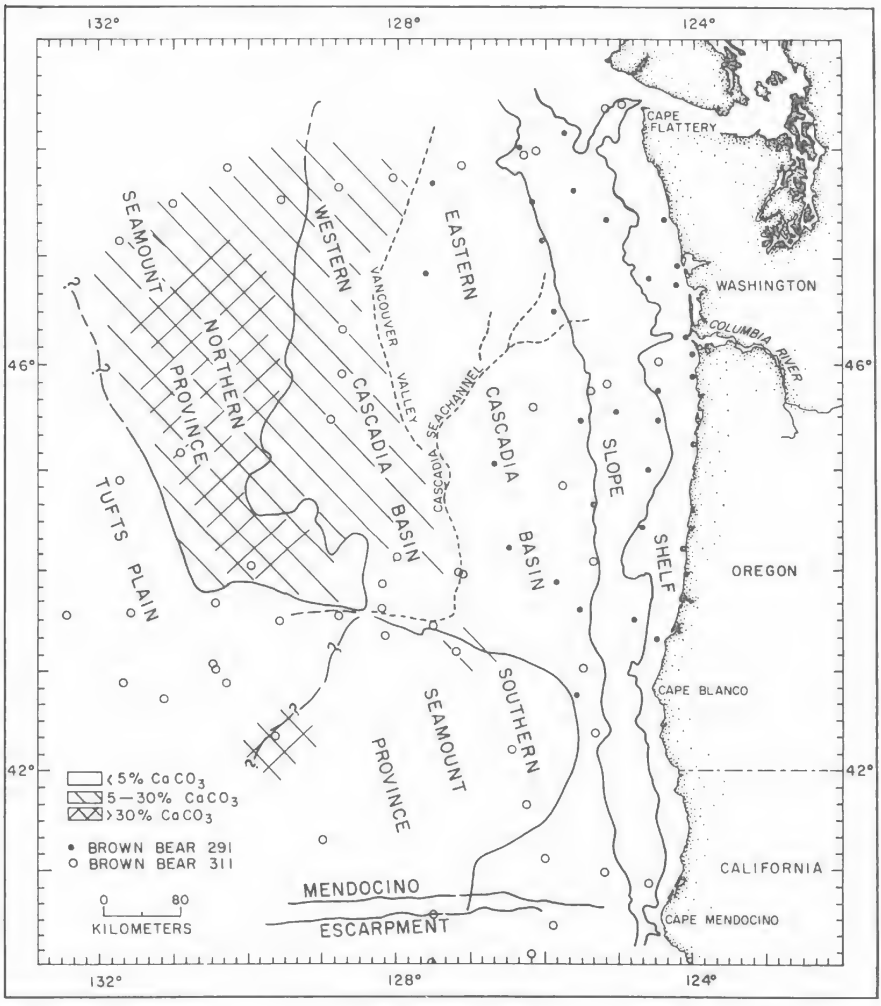

Figure 1. Distribution of $CaCO_3$ in surface sediment in part of the Northeast Pacific Ocean. Approximate boundaries of the major physiographic provinces are shown (McManus, 1964; Hurley, 1964).

Analytical Techniques

Samples (Figure 1) were collected from the R/V BROWN BEAR in August 1961 (Cruise 291) and August 1962 (Cruise 311). In order to limit the study to modern sediment, only the top one to three centimeters was taken from the gravity cores and only the top layer of the sediment was taken when a grab sampler was used. Because of the varying rates of deposition, these samples doubtlessly represent different intervals of time; in areas with low rates of deposition the intervals sampled may include some pre-Holocene sediment.

Weighed samples of finely ground, unwashed, dried sediment were mixed with 10 per cent H_3PO_4 in a closed flask which was heated to remove CO_2 and then flushed with CO_2-free air. The gases were collected, and their CO_2 content was determined by taking the difference between the initial and final volumes of the gas after passing it through KOH. The results, corrected for variations in temperature and barometric pressure and calculated as $CaCO_3$, are reproducible to within 2 per cent of the value reported.

The data are plotted in Figures 2 and 3; the median values for each physiographic province are given in Figure 2.

Discussion

The sediments from the various physiographic provinces (Figure 2) may be grouped according to $CaCO_3$ content as follows: (1) low-carbonate sediment from the Beaches and Columbia River estuary (median value 0.4% $CaCO_3$) and Continental Shelf (median value 1.4% $CaCO_3$); (2) the sediments of the Continental Slope (median value 2.2% $CaCO_3$), Eastern Cascadia Basin (median value 2.2% $CaCO_3$), Tufts Plain (median value 2.4% $CaCO_3$), and the area near the Mendocino Escarpment (median value 2.3% $CaCO_3$); and (3) the high-carbonate sediments from Western Cascadia Basin (median value 5.7% $CaCO_3$) and the Seamount Provinces (Northern Seamount Province—10.5% $CaCO_3$, Southern Seamount Province—4.5% $CaCO_3$). This last group of high-carbonate sediments includes some which Nayudu and Enbysk (in press) classified as oozes because of their abundant Foraminifera.

The complex history and diverse origins of the sediments in the Columbia River Estuary, on the beaches, and on the Continental Shelf are reflected in the variability of their $CaCO_3$ content. Local sources of carbonate appear to be especially important in this area. Unfortunately there are too few samples to warrant a discussion of the factors controlling the carbonate content of these sediments.

Sediments from the Continental Slope, Eastern Cascadia Basin, Tufts Plain, and from near the Mendocino Escarpment have a similar $CaCO_3$ content (Figure 2), with median values between 2.2 and 2.4 per cent $CaCO_3$. Deposition of lithogenous sediment is probably the dominant factor controlling the carbonate content of the sediments in these areas. As previously mentioned, the Northeast Pacific Ocean receives the runoff of the Columbia River as well as numerous, coastal rivers; thus there appears to be a plentiful supply of lithogenous sediment. The uniform carbonate content of these sediments can be explained as the result of a high rate of deposition of lithogenous sediment, containing 2 to 2.5 per cent $CaCO_3$, which is much greater than the rate of deposition of calcareous biogenous constituents. Consequently local variations in the carbonate content of the sediments are obscured.

The variability of $CaCO_3$ content of the Northeast Pacific sediments is probably caused, at least in part, by local topography which can have a profound influence on the type of sediment deposited at a given spot on a hilly or mountainous sea floor (Menard, 1964). Topographically low areas may be affected by turbidity flows whereas nearby slightly higher areas probably receive only the sediment settling down through the overlying water.

For example, the $CaCO_3$ content of the sediments from the Seamount Provinces and Western Cascadia Basin is clearly outside the range of $CaCO_3$ content of sediment in adjacent areas (Figures 2 and 3). In these areas the ocean floor is somewhat protected from the deposition of lithogenous materials transported along the bottom (Menard, 1955). Vancouver Valley and Cascadia Seachannel tend to channel turbidity currents away from Western Cascadia Basin and onto Tufts Plain.

Topographic effects are most evident in the Seamount Provinces where much of the sediment accumulates by particle-by-particle settling through the overlying water column or from the downslope movement of sediment from the seamounts. Where the supply of lithogenous sediment is limited to the material carried in suspension, the calcareous tests of foraminifera locally constitute more than 50 per cent of the sediment (Nayudu and Enbysk, in press).

The marked decrease in the $CaCO_3$ content of the sediments from the Seamount Provinces at depths between 3,100 and 3,300 meters (Figure 3) is probably also caused by dilution of the calcareous constituents with low-carbonate lithogenous sediment. Those sediments with the greatest carbonate content occur on topographic highs where the calcareous biogenous constituents

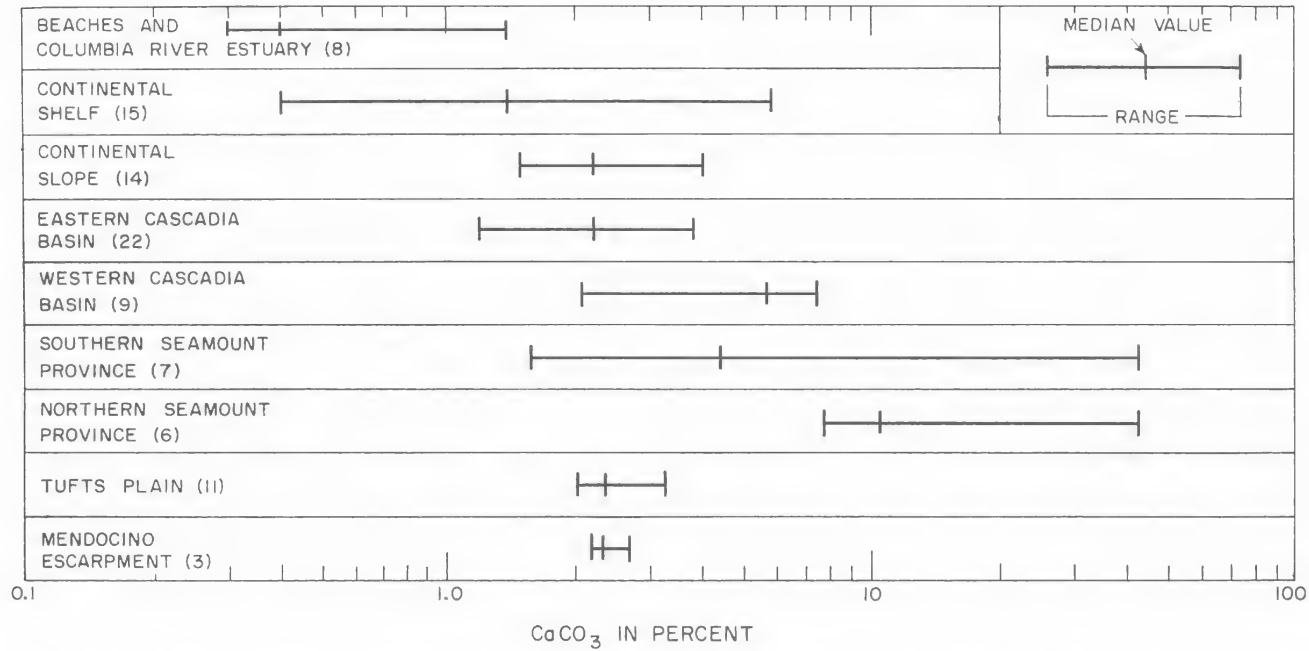

Figure 2. Range and median value of the $CaCO_3$ content of surface sediment from each of the major physiographic provinces in part of the Northeast Pacific Ocean. The number of analyses for each province is given after the name of the province.

are little diluted by lithogenous sediment, whereas sediments deposited on the plains include large amounts of low-carbonate sediment.

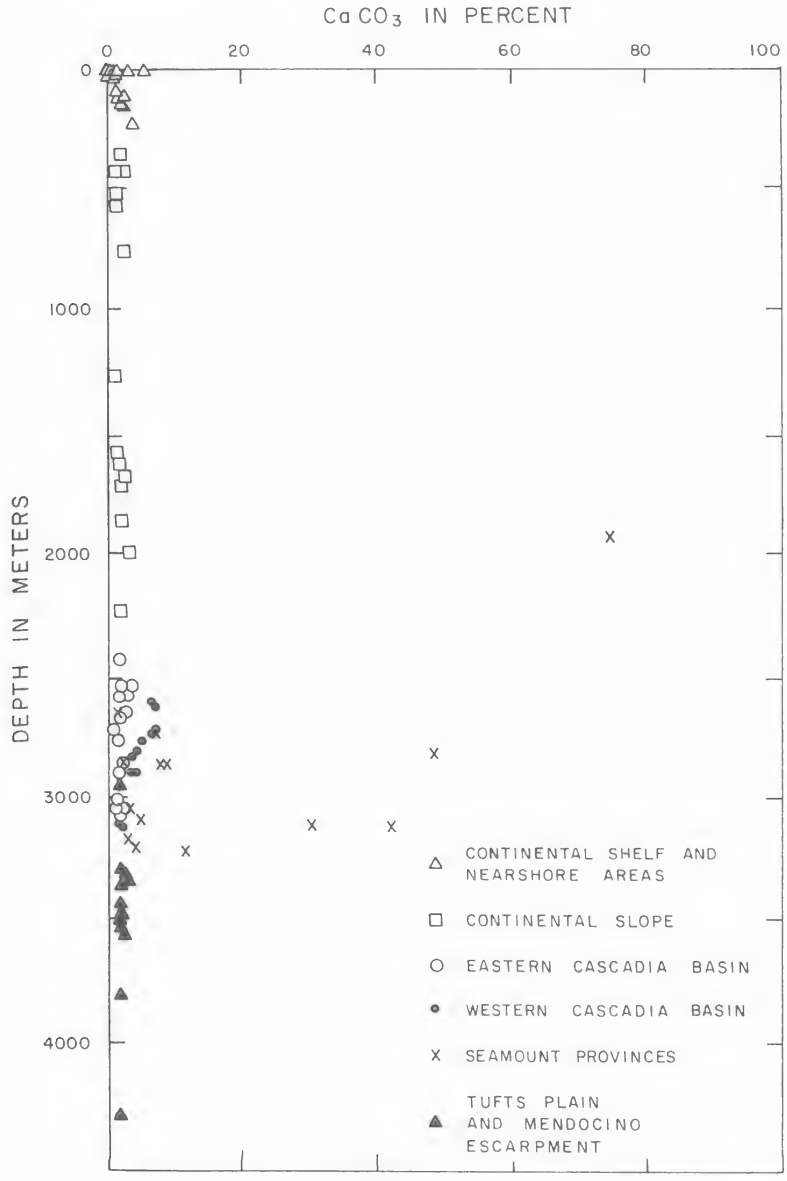

Figure 3. Distribution with depth of the $CaCO_3$ content of surface sediments in part of the Northeast Pacific Ocean.

There is no evidence indicating removal by solution of $CaCO_3$ from the sediments to a depth of 3,600 meters. Nayudu and Enbysk (in press) observed no globigerinids in the surface sediment at depths greater than 4,000 meters and concluded that removal by solution of foraminiferal tests is a significant factor at depths greater than approximately 4,500 meters. The observed marked decrease in the $CaCO_3$ content of the sediments at approximately 3,200 meters (Figure 3) occurs almost 1,000 meters above these depths where Nayudu and Enbysk observed pronounced solution effects and is probably caused by the greater rate of deposition of low-carbonate sediment in the deeper portions of the Seamount Provinces.

Thus, bottom topography appears to be a major factor controlling the rates of deposition and the $CaCO_3$ content of the sediments deposited in much of the area studied. That this is not the complete answer is obvious from the marked differences in the carbonate content (Figures 1 and 2) of the sediments of the Northern and Southern Seamount Provinces. Among other factors, it will be profitable to consider the deposition rates of siliceous marine organisms in future studies of the chemistry of Northeast Pacific sediments.

Summary and Conclusions

1. Modern marine sediments near the coast of Washington and Oregon generally contain less than 3 per cent $CaCO_3$. Sediment containing more than 5 per cent $CaCO_3$ is found only in the Northern Seamount Province and the western part of Cascadia Basin. It is inferred that the $CaCO_3$ content is low and rather uniform over most of the area because lithogenous sediment, containing little carbonate, is deposited much more rapidly than the calcareous remains of marine organisms.

2. There is no evidence to indicate that solution of carbonate controls the amount of $CaCO_3$ in the sediments deposited at depths less than 3,600 meters.

Acknowledgments

I wish to thank my colleagues B. J. Enbysk, D. A. McManus, Y. R. Nayudu, and J. S. Creager for many stimulating discussions and for their assistance. The analyses were performed by Mr. R. Shrack and Mr. Rex Couture.

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Geology of the South End of the Oregon Coast Range Tertiary Basin

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THE EOCENE strata at the south end of the Coast Range Tertiary Basin are divided into the Umpqua and Tyee Formations, and their general distribution is shown on the Geologic Map of Western Oregon (Wells and Peck, 1961). As a result of regional study of the Eocene stratigraphy, Baldwin (1963, 1964b) divided the Umpqua Formation into lower, middle, and upper members, "whose type sections are in the Camas Valley and Roseburg quadrangles. When these areas have been examined in more detail, and the sections measured adequately, the writer plans to give formal formational names to these units." The lower Umpqua member is steeply folded and faulted along trends paralleling those of the pre-Tertiary deformation of the Klamath Mountains. It is preserved only in narrow downfaulted troughs in the southern end of the basin. The middle Umpqua member overlies the lower member and oversteps onto the pre-Tertiary strata. The upper Umpqua member is present in the center of the basin between Agness and the Middle Fork of the Coquille River, and in a small area along the Sixes River.

The writer's interest in the southern end of the Coast Range Tertiary Basin began in 1943 while mapping in the Coos Bay coalfield for the State Department of Geology and Mineral Industries. In 1954 he mapped Eocene contacts for the U.S. Geological Survey in preparation for the state geologic map, and during the summers of 1961 and 1962 he worked in the Coquille and Bandon Quadrangles also for the U.S. Geological Survey. Later reconnaissance was supported in part by the State Department of Geology and Mineral Industries and the University of Oregon Faculty Research Funds. The writer is indebted to F. G. Wells, R. G. Wayland, and Parke D. Snavely of the U.S. Geological Survey and H. M. Dole of the State Department of Geology for the opportunity to work in the area. Mr. Dole provided information on the position of the Eocene basal contact in the Dutchman Butte Quadrangle.

Diller (1898, 1903) named and mapped the Umpqua and Tyee Formations in the Roseburg, Coos Bay, and Port Orford areas. Allen and Baldwin

(1944) revised the geology of the Coos Bay area. Turner (1938) described the faunas and measured sections of the Umpqua and Tyee Formations, one of them being along the Middle Fork of the Coquille River.

Lower Umpqua Member

The lower Umpqua member as defined by Baldwin (1963, 1964b) crops out in the southern part of the Coast Range. It consists of graywacke turbidites and basaltic pillow flows and breccias. There are few places where the writer can designate the base of the lower Umpqua with assurance for wherever it is in contact with pre-Tertiary rocks it is either faulted or the relationship is obscure. Many of the conglomerates that are supposedly basal Umpqua are in reality the base of the middle member.

Burns (1964) measured the thickness of the Umpqua Formation along the Middle Fork of the Coquille as 11,200 feet; of this, he assigned 2,700 feet to the lower member, about 6,000 feet to the middle member, and 2,500 feet to the upper member. He noted that part of the lower unit has been omitted by faulting. Burns' Middle Fork section is partly within the mapped area and partly just to the north in the Sitkum and Coquille Quadrangles. Rau and Baldwin (unpublished) measured and sampled the Rock Creek section south and west of Bone Mountain. They found 10,750 feet of Umpqua section, and the lower part was incomplete and faulted.

In the Coos Bay area, volcanic rocks that are a part of the lower member of the Umpqua Formation crop out on Blue Ridge, on the hill a short distance south and east of Coquille, and on Sugarloaf Mountain east of Myrtle Point. A small amount of volcanic rock interfingers with the lower Umpqua sedimentary rocks in the northeastern corner of the Powers Quadrangle. The writer concludes that all the basaltic flows and breccias of the Umpqua Formation are confined to the lower member.

The lower member is preserved in a fault-bounded trough at the south end of the Coos Bay coalfield which extends into the northwestern part of the Powers Quadrangle, and in a fault block extending southward to the vicinity of Gaylord (Figure 1). The beds are typically thin, flysch-like, rhythmically bedded graywacke without basalt flows except in the area northeast of Gaylord. Other lower Umpqua outcrops include beds along the Rogue River between Illahe and Agness, and in an isolated fault trough along Fourmile Creek in the northern part of the Langlois Quadrangle and small patches at Cape Blanco and a short distance north.

Beds assigned to the lower Umpqua near "Masons Wall," four miles north of Agness, are rhythmically bedded, dark-gray graywacke, commonly in

beds of one foot or less thickness. Conglomerate, presumably at the base of the section, crops out along Twomile Creek just east of the fault contact between Tertiary and older rocks. The section near the "Masons Wall" is approximately 4,000 feet thick where exposed in Twomile Creek and the Rogue River. Here, the lower Umpqua is either overlain unconformably by middle Umpqua strata or faulted against the Middle Umpqua just north of Illahe. An inferred fault contact is shown, but the evidence is not conclusive (Figure 1).

The lower Umpqua in the Fourmile Creek fault block in the northern part of the Langlois Quadrangle is separated but a short distance from the Coos Bay Basin. The strata include both massive and pebbly sandstones as well as thin-bedded graywacke.

Eocene beds were reported from Cape Blanco by Bandy (1944) in the sheared rock just east of the lighthouse. Bandy considered the fauna to be middle Eocene, but it is likely that the beds are a part of the lower Umpqua, similar to steeply dipping beds in Morton Butte a short distance to the north. Dott (1962) described the geology of the Cape Blanco area, and referred to beds of probable Late Cretaceous age a short distance north of the mouth of the Sixes and noted their general resemblance to Eocene rock. They are included in the lower Umpqua member in this report. Lower Umpqua strata are generally involved in the shearing that followed the deposition of that unit, and therefore the Eocene strata in the vicinity of Cape Blanco seem best assigned to that unit.

Structural trends in the pre-Tertiary units near the Oregon-California border are in the form of an arc (*e.g.* King, 1959) convex to the west. Trends shown on Figure 1 are at a point on the arc where the north-trending faults and folds tend to swing northeastward. Along the northern flank of the arc near Roseburg, the structural trends are commonly N 45 to 75° E.

Age and Correlation

Megafossils are relatively rare in the lower Umpqua strata, but microfossils are present in many specimens. Foraminifera from the lower Umpqua generally are considered to be lower and perhaps middle Eocene, comparable to the Capay beds of California. They have been assigned by Rau (written communication) to the C and lower B zones of Laiming or the Penutian stage of Mallory (1959) although some have Paleocene affinities.

Fresh samples were obtained with a power auger by the Standard Oil Company of California along the North Fork of the Coquille River, two miles northeast of Myrtle Point in the Coquille Quadrangle (NE ¼ sec. 10, SW¼ sec. 11, T. 29 S., R. 12 W.), and in the vicinity of Gravelford (SW ¼

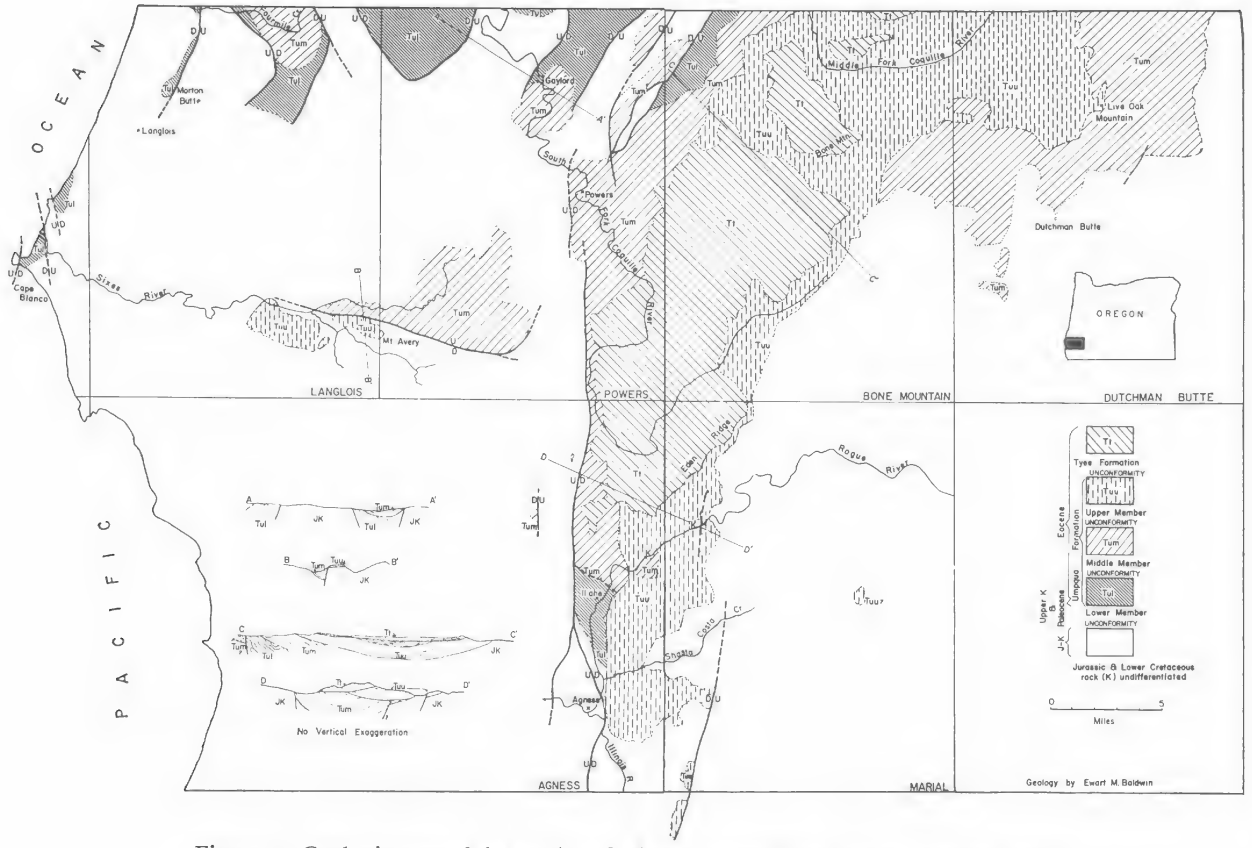

Figure 1. Geologic map of the south end of the Oregon Coast Range Tertiary basin.

and NE ¼ sec. 25, T. 28 S., R. 12 W.). Some of these samples were considered to be Late Cretaceous, probably Campanian and Maestrichtian. A sample from the northwest tip of Cribbins Hill, another taken two miles northeast of Gravelford, and some beds associated with the top of the basalt unit north of Myrtle Point were considered to be Paleocene. Some of these samples were examined by Rau (written communication) who confirmed the presence of Late Cretaceous and Paleocene faunas.

The strata in question are thin-bedded graywacke that cannot be separated lithologically or structurally from the lower Umpqua. They lie in a zone of intense deformation, paralleling the North Fork of the Coquille River, that mask their original structural relationships. Blocks of greenstone, schist, and serpentine, some large enough to quarry, are included within this shear zone. The basalt of the lower member is commonly found at or near the base of the formation where exposed, but a sedimentary section of varying thickness containing Late Cretaceous beds could be present beneath the basalt within the basin.

Beds of Campanian and Maestrichtian age resembling the lower Umpqua are known to occur at Cape Sebastian (Howard and Dott, 1961). In the absence of known unconformities within the section, it seems best to consider the Campanian and Maestrichtian beds along the North Fork of the Coquille, and possibly those at Cape Sebastian, as the basal part of the lower Umpqua member with nearly continuous deposition through the early Eocene.

Post-Lower Umpqua Deformation

At the end of early Eocene time the lower Umpqua beds were steeply folded and downfaulted into troughs. Intervening areas were uplifted, and thick sections of the lower Umpqua and pre-Tertiary rocks were removed. It is difficult to determine the original extent of the lower Umpqua basin, but it presumably covered more area than any of the succeeding Tertiary units.

Middle Umpqua Member

The sea reoccupied the southwestern Oregon basin following truncation of lower Umpqua and pre-Tertiary strata. The basal middle Umpqua beds are massive conglomerates with pebbles of chert, quartz, graywacke, greenstone, and intrusive rock in varying proportions depending upon the composition of nearby highlands. Sandstone and siltstone are more common higher in the section. The thicker sections of middle Umpqua are confined to faulted basins, some of which coincide with those established earlier.

One of the largest areas of middle Umpqua strata is between the Rogue River near Illahe and the South Fork of the Coquille at Powers. The area

is bounded on the west by a prominent normal fault that extends from Agness to a point west of Powers where it is offset westward. The northern segment has considerably less throw, and it either dies out northward or turns northeastward paralleling other faults in the northern half of the Powers Quadrangle.

The basal conglomerate changes rapidly upward into dark-gray rhythmically bedded graywacke which, though less steeply dipping, less well jointed, and indurated, resembles the beds in the lower Umpqua. Born (1963) determined the thickness of the Umpqua in the Powers area to be 7,600 feet, all of which the writer assigns to the middle member. Burns (1964: 23) measured 6,000 feet of middle Umpqua along the Middle Fork of the Coquille. Of this, the conglomerate and sandstone make up the lower 4,000 feet. Burns found that the pebbles consist of chert, metavolcanic rock, vein quartz, metasedimentary rock, basalt, and quartzite in approximate order of abundance.

The eastern edge of the middle Umpqua must thin rapidly east of Illahe, for a very thin section surrounds the Cretaceous beds at Tacoma Rapids a short distance up the Rogue River from Illahe. Faulting and erosion of middle Umpqua beds must have occurred along the eastern margin prior to deposition of the upper member (Figure 1, sec. D-D′).

A thick section of middle Umpqua is preserved in a fault basin at the head of the Sixes River (Figure 1, sec. B-B′). The basal conglomerate in this section is relatively thin and grades upward rapidly into pebbly sandstone and thin-bedded sandstone and siltstone. The total thickness is estimated to be 2,500 feet. Diller (1903) reported coal in this basin, which indicates proximity to shoreline, and interfingering relationship with non-marine strata. The dip of the beds steepens at the western end of the basin near the Sixes River fault where the beds appear to have been overlain unconformably by less-steep beds of the upper member (Figure 1, sec. B-B′).

A semicircular basin containing middle Umpqua with a total thickness of approximately 600-1,000 feet crops out at Gaylord in the Powers Quadrangle (Figure 1, sec. A-A′). The basal conglomerate and massive pebbly sandstone form a prominent cliff approximately 200-250 feet high along the northern, eastern, and southern rim; thin-bedded sandstone and siltstone occur in the center of the basin.

An oval basin filled with middle Umpqua strata overlies the lower Umpqua along Fourmile Creek. The basal conglomerate is thin or missing, but massive sandstone takes its place, and the beds grade upward into rhythmically bedded, dark-gray, sandy siltstone.

Age and Correlation

Allen and Baldwin (1944: 14) list megafossils collected along Fourmile Creek from sections 10 and 11, T. 30 S., R. 14 W. from beds herein assigned to middle Umpqua strata. Thoms (1964) identified orbitoids and smaller Foraminifera from a locality near the base about 500 feet west of the mouth of Little Creek. He concluded that they were Penutian, similar to the C zone of Laiming, an age slightly older than the writer assigns to the middle Umpqua strata. Thoms dated the beds in the Powers area as middle Eocene, late Penutian, and Ulatisian. He found it difficult to zone the Umpqua Formation closely on the basis of Foraminifera. Some strata considered by the writer to be lower Umpqua contained Foraminifera that appeared to represent the middle B zones, whereas beds considered to be middle Umpqua contained Foraminifera that appeared to be as old as C zone of Laiming, or Penutian of Mallory (1959). Similar results have been reported by others working on the Umpqua microfossils. The ultimate division of the units will rest on stratigraphic evidence.

Post-Middle Umpqua Deformation

Deformation, although minor compared with post-lower Umpqua folding, was followed by erosion of large areas of middle Umpqua strata. A few isolated patches of middle Umpqua sedimentary rocks indicate that the beds were once more widespread. Post-middle Umpqua faults, such as the one between Agness and Powers, helped preserve middle Umpqua strata along their downdropped sides. Much of the movement evidently took place before the deposition of the less steeply dipping upper Umpqua beds.

Upper Umpqua Member

The upper Umpqua strata crop out between Agness and the Middle Fork of the Coquille River and along the Sixes River.

The upper Umpqua is well exposed along Highway 42 paralleling the Middle Fork of the Coquille River. Here Burns (1964) measured 1,400 feet of sandstone overlain by 1,200 feet of mudstone. He found the sedimentary structures in this member much like those in the sandstone and conglomerate of the middle member. Thin lamellae of coal in graywacke sandstone occur in outcrops that also show both large- and small-scale cut-and-fill structures, and cross-bedding. The uppermost beds of upper Umpqua, beneath the Tyee sandstone which caps Bone Mountain, are medium- to dark-gray mudstone. The upper member contains mollusca throughout and abundant Foraminifera, particularly in the upper mudstone.

The upper Umpqua is exposed along the Rogue River between the mouth of Shasta Costa Creek near Agness, and the mouth of Tate Creek five miles

up the Rogue River from Illahe. It is composed almost entirely of conglomerate and pebbly sandstone; medium- to fine-grained sandstone and siltstone are restricted to the uppermost part of the member. Approximately 2,750 feet of upper Umpqua beds are present in the syncline between the mouth of Watson Creek and the unconformably overlying Tyee Formation in Eden Ridge. The basal conglomerate of the upper member contains pebbles ranging from three to six inches in diameter; in places along the old shoreline considerably larger boulders of subjacent formations are present. The conglomerate along the lower part of Shasta Costa Creek contains many pebbles of diorite similar to rocks cropping out in the Illinois River drainage. The upper Umpqua is faulted against the Dothan Formation along the east side of the fault trough across and south of Shasta Costa Creek. The fault appears to have a throw of approximately 500 to 1,000 feet.

Coal is present near the mouth of Shasta Costa Creek, and some of the marine upper Umpqua evidently interfingered with non-marine strata along the margin of the basin.

The upper Umpqua of the Sixes River is largely conglomerate and massive sandstone that grades upward into lesser amounts of thinner-bedded sandstone and siltstone. The section exposed in and near Mt. Avery is about 500-600 feet thick. The unit lies along the south side of the Sixes River fault, but it evidently rested unconformably on the downfaulted middle Umpqua prior to erosion of the Sixes River valley (Figure 1, sec. B-B′). Conglomerate at the base along the south side west of Mt. Avery is made up of rounded boulders of Cretaceous grit and pebbles reworked from the underlying Lower Cretaceous conglomerate. Fossils have not been found, but the beds compare in lithology, position, and texture with upper Umpqua strata along the Rogue River. The conglomerate is much thicker and the pebbles are less well rounded than the underlying middle Umpqua conglomerate, and therefore doesn't appear to be an unfaulted equivalent.

Age and Correlation

The age of the upper Umpqua is apparently middle Eocene. Foraminifera from the upper part of the Rock Creek section near Bone Mountain were considered to be in the upper B zones or Narizian by Rau (written communication). Its position between the middle Umpqua and the Tyee Formation also points to a middle Eocene age.

Wells, Hotz, and Cater (1949) found megafossils between the forks of Indigo Creek southeast of Agness. Ralph Stewart of the U.S. Geological Survey concluded that they were equivalent to the "Arago Formation." The writer considers them to be in the upper Umpqua and to be middle Eocene.

Tyee Formation

The Tyee Formation is present in a relatively shallow syncline near the heart of the Coast Range extending southward through Bone Mountain where approximately 500 feet is present to Eden Ridge where perhaps 2,500 feet is preserved in the center of the basin. The formation has been cut through by the Middle Fork of the Coquille and its tributaries to the south.

The Tyee Formation was laid down following crustal warping during which time some of the upper member of the Umpqua was removed. The Tyee Formation rests on all three members of the Umpqua Formation in various parts of southwestern Oregon.

In the center of the Coast Range to the north of the mapped area the Tyee Formation is generally micaceous, rhythmically bedded sandstone. Beds near the southern tip of the Tertiary Basin are thicker and lack the characteristic rhythmic bedding and abundant mica. Beds of conglomerate are also present. Coal and fossil wood suggest deposition near the margin of the basin where conditions were not favorable for forming graded bedding.

Baldwin (1961), discussing the Elkton Siltstone Member of the Tyee, reviewed known Tyee fossil localities and indicated that they were not in the massive part of the formation but were, in fact, in the Elkton Member or in its equivalent such as the beds at Lorane and Sacchi Beach. Megafossils were found a short distance stratigraphically above the massive Tyee both at Basket Point and Elkton along the Umpqua River, but Foraminifera were scattered all through the Elkton and Sacchi Beach Members.

Tectonic History

A summary of the tectonism of the southern end of the Coast Range depends in part on evidence collected in nearby regions, much of it in the Coos Bay and Roseburg areas. Deformation following deposition of the lower Umpqua member produced steeply dipping strata which are preserved in fault troughs. In addition to steep faults bordering the troughs, Baldwin (1964b) proposed northwestward thrusting in the Roseburg area, and similar thrusting is postulated east of Myrtle Point along the North Fork of the Coquille River where the basalt of Sugarloaf Mountain appears to be thrust northwestward. Blocks of peridotite, greenstone, and other pre-Tertiary rocks crop out in the fault zone. Whether lateral movement also took place is not known. This thrust zone, like most of the steep border faults bordering the lower Umpqua, is overlain unconformably by the middle Umpqua strata without significant displacement of the younger unit. The post-lower Umpqua deformation was the most intense, and the erosional break following of greater magnitude, than any of the succeeding breaks in the Paleocene-Eocene section.

Normal faulting followed deposition of the middle Umpqua, and notable examples are the Agness to Powers fault and several south and west of Roseburg.

Faulting of perhaps lesser magnitude followed deposition of the upper Umpqua member. A fault with perhaps 500 to 1,000 feet throw borders the upper Umpqua along the eastern margin of the Rogue River trough from the Illinois River nearly to the Rogue.

Few well-defined faults were found within or along the margin of the Tyee Formation although faults with throws on the order of 100 feet might have been overlooked. The location of the basins of deposition may coincide with fault troughs as shown by remnants of both middle and upper Umpqua strata.

The trend of the normal faults may be controlled by deep-seated fracture zones initiated during pre-middle Umpqua deformation, paralleling trends in the Klamath Mountains. Major shearing and thrust faulting appear to affect only the lower Umpqua and older strata in southwestern Oregon.

Within the town of Bandon along the coast and north of the mapped area, late Eocene Coaledo beds are present in juxtaposition with pre-Tertiary strata (R. E. Stewart, verbal communication) indicating that the block near the coast was either a positive area during deposition of the Umpqua and Tyee Formations or post-Tyee uplift caused removal of all earlier Tertiary strata prior to deposition of Coaledo sedimentary rocks. If the latter is true, this coastal block may have remained active longer than blocks to the east.

Oligocene and Miocene strata are not known in the Bandon area, but Mio-Pliocene sedimentary rocks are present at Cape Blanco and along Coos Bay. Abundant Pliocene fossils are washed up on the beach at Bandon, and Baldwin (1946a: 40) suggests that Pliocene, and possibly Miocene, strata are more or less continuous offshore between known strata of similar age at Cape Blanco and Coos Bay. The younger Cenozoic strata along the coast exhibit only normal faulting of moderate displacement.

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A Soil Sequence from Southwestern Umnak Island, Alaska

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AS A PART of a comparative investigation of the ecology and prehistory of Konyag Eskimo and Aleut peoples, which has been carried on since 1961 by the University of Wisconsin (Laughlin and Reeder, 1962a), a study has been made of the soil near the ancient Aleut village site of Chaluka, on the southwestern coast of Umnak Island, Alaska. Situated on Nikolski Bay, a broad reentrant of the Bering Sea, the Chaluka mound, bordering the present village of Nikolski on the south, has been excavated repeatedly and the archaeological remains analyzed (Laughlin and Marsh, 1951; Reeder, 1962; Laughlin, 1963). Soil profiles have been examined along a transect running up a south-facing slope immediately northeast of Nikolski (Figure 1), thereby providing knowledge of the sequence of buried soils on the southwestern end of the island. The stratigraphic section of Chaluka and a series of pollen profiles are presently under study and will be compared with these sections.

Geography and Geology

Umnak Island, as a major member of the Fox Island group rising from the Aleutian ridge near the base of the Alaska Peninsula, lies approximately between the parallels 52° 50′ and 53° 34′ north latitude, and meridians 167° 47′ and 169° 7′ west longitude. The main island is about 71 miles in length and 17 miles in greatest breadth; it separates the Bering Sea on the northwest from the Pacific Ocean on the southeast. The northeast end of Umnak, nearly divided at Inanudak Bay from the remainder of the island, is quite regularly conical, having been formed by Quaternary lava outflow from Okmok Volcano, now depressed centrally as the remarkable Okmok caldera. The south-central mass of the island, of greater relief and much more complex in physiognomy, is dominated by the two glaciated volcanic peaks of Mount Vsevidof (2109 M.) and Mount Recheschnoi (1984 M.), at least the former of which has erupted in historic time. To the southwest

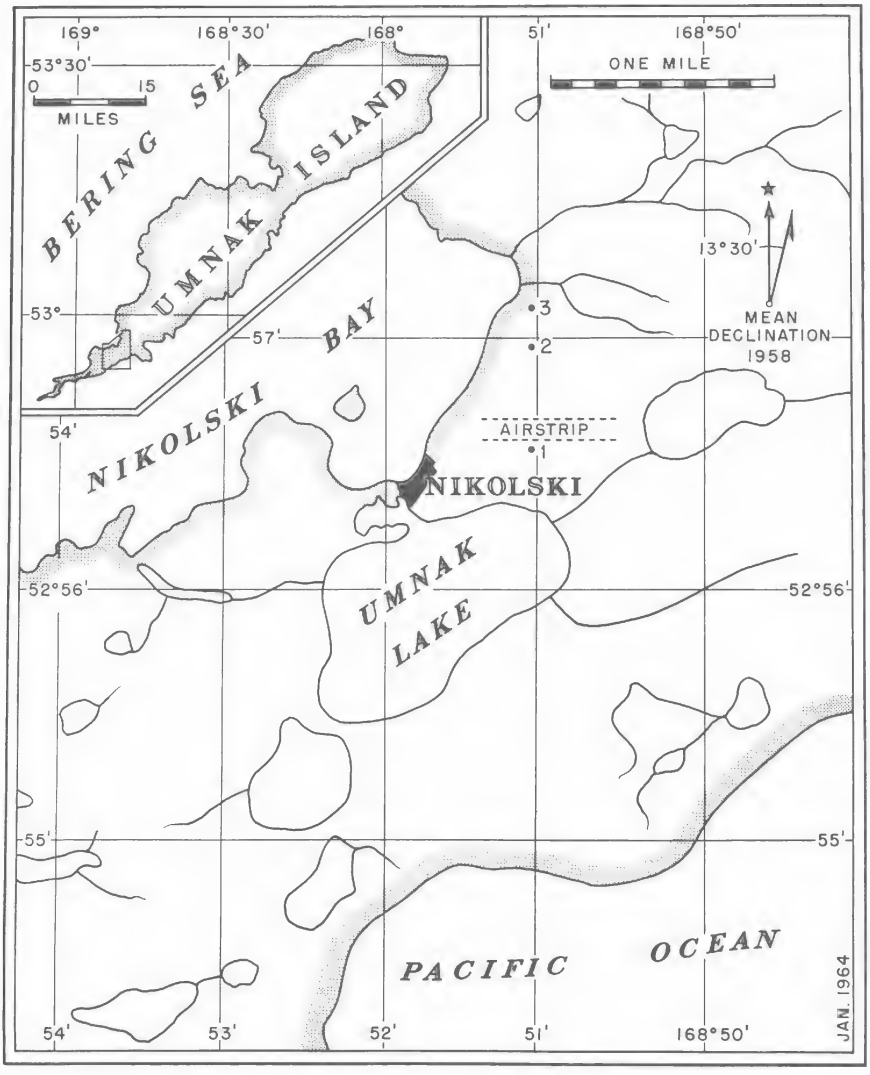

Figure 1. Umnak Island, western Nikolski Plain; positions of described soil profiles are numbered on transect perpendicular to the Nikolski airstrip. Chaluka archaeological site is located along southwestern margin of Nikolski village.

of this mountain mass, the gently undulating Nikolski Plain runs to Cape Sagak at an average altitude of about 300 feet, supporting a number of small, shallow, but presently permanent lakes (Byers, 1959). The deep soil sections here described pertain to this broad plain, on the Bering shore of which the Aleut village (now Nikolski) has existed more or less continuously for a period in excess of 4000 years (Laughlin and Reeder, 1962b; Black and Laughlin, 1964). Other village sites, recently but not presently occupied, are distributed on the coastal perimeter of this plain.

The Nikolski Plain is underlain principally by a complex of albitized sedimentary and igneous rocks which appear to have formed and become altered in the early and middle Tertiary, although some rocks may be older. Post-Oligocene intrusive dioritic plutonics underly the Quaternary volcanics of Mount Vsecidof and Mount Recheschnoi and reach the surface in the northern section of the piedmont, although not apparently in the region of the soil profiles. Byers (1959) has described and mapped an "older glacial till" of probable Wisconsin age on the slopes of the volcanoes where it is overlain in places by a younger and unweathered till of Recent formation associated with existing glaciers. Sporadic outliers of "older till," which overlie unconformably the bedrock of the plain itself, are discussed by Byers but are not mapped. Weathered till, presumed to be the same, has been found at the bottom of all pits dug in the present study in the vicinity of Nikolski.

Recency of development of the landform of the Nikolski Plain through the action of a later Pleistocene piedmont glacier extending to and beyond the offshore island of Anangula (Ananiuliak on charts of U.S. Coast and Geodetic Survey) is suggested by immaturity of drainage pattern. Most of the many small lakes are of centripetal drainage, but where outlets have formed, the cut banks have not yet become obliquely eroded (Byers, 1959).

Climate

The climate is marine subarctic (U.S. Coast Pilot, 1955) and is characterized by overcast skies, high winds, and small variations in diurnal temperature; fog and drizzle or light rain are typical. Winds of gale force or stronger are common, especially in the winter months. Summer temperatures range from 46° to 68° F.; winter temperatures average slightly above freezing at sea level. There is no permafrost. The following chart gives data on Nikolski weather gathered between October, 1942, and April, 1945 (Byers, 1959).

Temperature (degrees Fahrenheit):	
Mean annual	39.2
Maximum annual	64.0
Minimum annual	11.0
Precipitation (Inches):	
Mean annual	41.19
Annual snowfall, unmelted	49.9
Greatest depth on ground	13.0
Number of days with at least trace of precipitation	307
Fog: Annual percentage of occurrence	13.0
Wind (Miles per hour):	
Average velocity	19.4
Extreme velocity	72.0
Sky (condition in per cent of hours):	
Clear	1.7
Scattered or broken	34.5
Overcast or obscured	63.8

Vegetation

The vegetation typically found on the soils described here varies with position on the slope (Kindschy and O'Connell, 1959). The exposed, wind-swept area at the top of the rolling hills is covered by a low heath community, composed chiefly of *Empetrum nigrum* (crowberry) together with considerable intermixture of *Deschampsia beringensis* (Bering hair-grass). Other species found commonly in this community are *Listera cordata* var. *nephrophylla* (heartleaved twayblade), *Campanula lasiocarpa* (mountain harebell), *Achillea borealis* (northern yarrow), *Claydonia* sp. (lichens), and moss. Less commonly is found *Salix reticulata* ssp. *orbicularis* (willow).

The vegetation on the long, well-drained slopes below the hill top is dominated quite completely by a community of *Deschampsia beringensis* with interspersed sedges (*Carex* sp.). Also common here are *Trientalis europaea* (star flower), *Viola langsdorfii* (Alaska violet), *Achillea borealis,* and *Coptis trifoliata* (trifoliate goldthread). Typical, although far less common, are *Conioselinum benthami* (western hemlock-parsley), *Angelica lucida* (sea coast angelica), and *Aconitum maximum* (Kamchatka aconite). In moist seeps on the slopes and with lesser density along the drainages *Equisetum arvense* (common horsetail) grows as an important subdominant of the community (Anderson, 1959).

Soils

Due to recurrent ash falls, actual sources of which are not certain, there are several lithologic discontinuities in each soil profile. The underlying bedrock is a gray to greenish-gray argillite which is jointed and layered when found close to the surface. In the sequence described here, bedrock approaches the surface only at the top of the hill, where the almost constant wind apparently scoured off ash that fell here leaving only the thin layer of till and about 40 cm. of soil over the bedrock. The till layer, formed primarily of coarse fragments of argillite, becomes thicker downslope. At the upper surface of the till is observed a lag concentrate, also composed mainly of argillite fragments, overlain by buried soil horizons and layers of ash. In the area investigated, the ash layers remaining buried in the section have not been of depth sufficient to have protected the buried soil from the continuing effects of root penetration, leaching, and weathering. Thus, each most recently buried soil has continued to change for a period of time after the subsequent ash fall. Modification of the buried soil has terminated or at least has become considerably slower when ash and new soil have accumulated to a depth of about 40 cm., since roots of plant species presently providing vegetative cover are concentrated at lesser depth. Thus the physical characteristics of the buried soils cannot be considered to have remained unchanged since the time of initial burial.

The zonal soils studied here have been placed in the great soil group "Tundra without Permafrost" as defined by Kellogg and Nygard (1951). They include in their report a relatively simple profile taken on the north end of Umnak Island. In the soil survey report covering northeastern Kodiak Island (Rieger and Wunderlich, 1960) these soils are tentatively classified as belonging to the Ando great soil group; in the Seventh Approximation they would be classified as Inceptisols (Soil survey staff, 1960). Ando soils typically have a thick, dark surface and are characterized by a very high (commonly more than 10%) organic content. Due to lack of information on the soils of Umnak Island, classification below the great soil group has not been attempted (for discussion of arctic soils see Tedrow *et al.,* 1958 and Soil Survey Manual, 1962).

In the descriptions of the soil profiles themselves numbers instead of letters are used because the variety and number of horizons make conventional designations cumbersome and less meaningful. In several cases slumping or solifluction has created complex horizons from a series of simpler ones. This is especially true in the first and second profiles described. Soil colors are based on Munsell color chips using moist samples under field conditions.

Measurements used in describing the profiles were taken on or near the vertical midline of the sections, as illustrated in the figures.

The first profile (see Figure 2) is located south of the airstrip at Nikolski

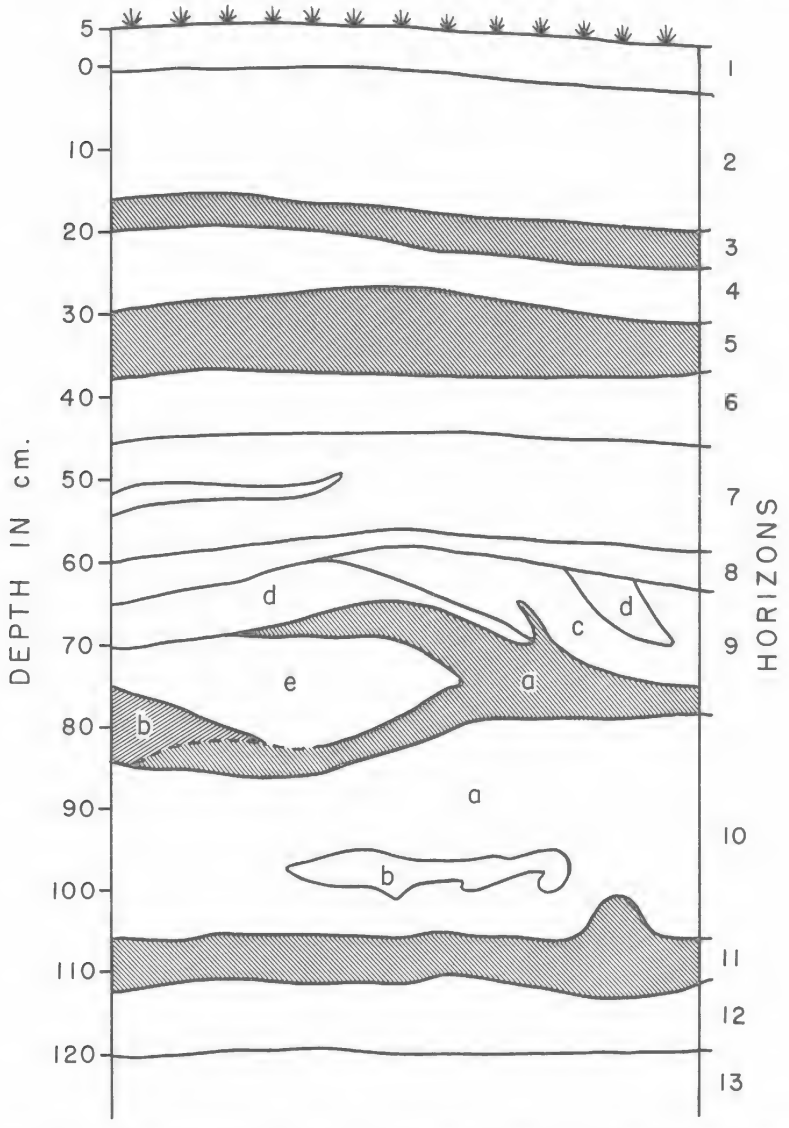

Figure 2. Diagrammatic view of soil profile no. 1. Shaded horizons are composed of volcanic ash; buried A and B horizons occur below each ash horizon. This profile, with four major ash layers, is typical of the Nikolski area. (Horizontal dimensions not to scale.)

although still within the fence which has separated the airstrip from range lands for a period in excess of 20 years. The soil at this point was not disturbed in the construction of the airstrip. Structural description has been omitted in the lower horizons because the minor structural variation cuts across horizons. For the most part, the structure of these lower horizons appears to be massive.

Soil Profile One (Figure 2)

Classification: Ando.
Location: 200 feet south of airstrip.
Description of site: Foot of 5% south-facing slope on piedmont plain.
Elevation: Approximately 50 feet.
Climate: Very humid.
Vegetation: Meadow; *Deschampsia beringensis* and *Carex* spp. predominant. Site has been grazed during historical times.
Root distribution: Most roots from 0-37 cm., some to 104 cm.
Parent material: Volcanic ash of variable texture and representing several falls, over glacial till at 120 cm.
Natural drainage: Moderately well drained. Ground water below 120 cm. at time of sampling.
Erosion: Probably no accelerated erosion, except immediately after ash falls, due to thick, unbroken sod.

Profile: Depth (in cm.)	Horizon	Description
5-0	1	Partially decayed grass roots and stems; matted and decayed lichens and mosses.
0-14	2	Black (5YR 2/1) silt loam; weak medium subangular blocky structure; firm moist; pH 6.0; clear wavy boundary.
14-20	3	Very dark brown (10YR 2/2) volcanic ash of sandy loam to loamy sand texture. Very weak granular structure; granules break readily into single grains; pH 5.5; clear wavy boundary.
20-26	4	Black (10YR 2/1) silt loam; weak to moderate medium to coarse subangular blocky structure; firm moist; pH 5.5; clear smooth boundary.
26-35	5	Very dark brown (10YR 2/2) volcanic ash of loamy coarse sand texture. Included yellowish red (5YR 4/6-4/8) grains; single grain; loose; pH 6.0; abrupt smooth boundary.
35-42	6	Dark brown (7.5YR 3/2) silt loam (?); weak, thick platy structure; friable moist; pH 6.0; clear wavy boundary.

42-56	7	Very dark brown (10YR 2/1.5) silt loam (?); common fine distinct yellowish-red (5YR 4/8) mottles; weak medium to coarse subangular blocky structure; firm moist; pH 6.0; a lens of very dark brown (10YR 2/2) silt loam was noted near the center of this horizon; clear wavy boundary.
56-60	8	Dark brown (10YR 3/3) silt loam (?); very weak medium subangular blocky structure; firm moist; pH 6.0; clear wavy boundary.
60-84	9	The following layers were noted between 60 and 84 cm.
	a	Dark brown (7.5YR 3/2) volcanic ash of coarse sandy loam texture; many fine to medium distinct yellowish-red (5YR 4/8) mottles; pH 6.5.
	b	Very dark brown (10YR 2/2) volcanic ash of sandy clay loam texture; pH 6.5.
	c	Very dark brown (10YR 2/2) silty clay, fine faint dark yellowish-brown (10YR 4/4) mottles; pH 6.5.
	d	Very dark brown (10YR 2/1.5) silt loam; pH 6.0.
	e	Very dark brown (10YR 2/2) clay loam; pH 6.0.
84-105	10	
	a	Dark brown (7.5YR 3/2) silty clay; pH 6.5.
	b	Dark reddish brown (5YR)/4) fine sandy clay loam; pH 6.5.
105-112	11	Dark Brown (7.5YR 3/2) volcanic ash of loamy coarse sand texture; many reddish-yellow pebbles; pH 6.5.
112-120	12	Very dark brown (10YR 2/2) silty clay loam; pH 6.5.
120-160+	13	Dark yellowish brown (10YR 3/4) glacial till.

The second profile (Figure 3) was dug north of the airstrip about half of the way up the slope under discussion. Again structures have been omitted for the lower horizons.

Soil Profile Number Two (Figure 3)

Classification: Ando.

Location: Approximately one-third mile north of the airstrip near the crest of the first ridge.

Description of site: Top of 2% southeast-facing slope on piedmont plain.

Elevation: Approximately 200 feet.

Climate: Very humid.

Vegetation: Meadow; *Deschampsia beringensis* and *Carex* spp. predominant. Site has been grazed by sheep.

Root distribution: Most roots from 0-35 cm., some 87 cm.

Parent material: Volcanic ash of variable texture and representing several falls, over glacial till at 108 cm.

Natural drainage: Well drained.

Erosion: Probably no accelerated erosion, except immediately after ash falls, due to thick, unbroken sod.

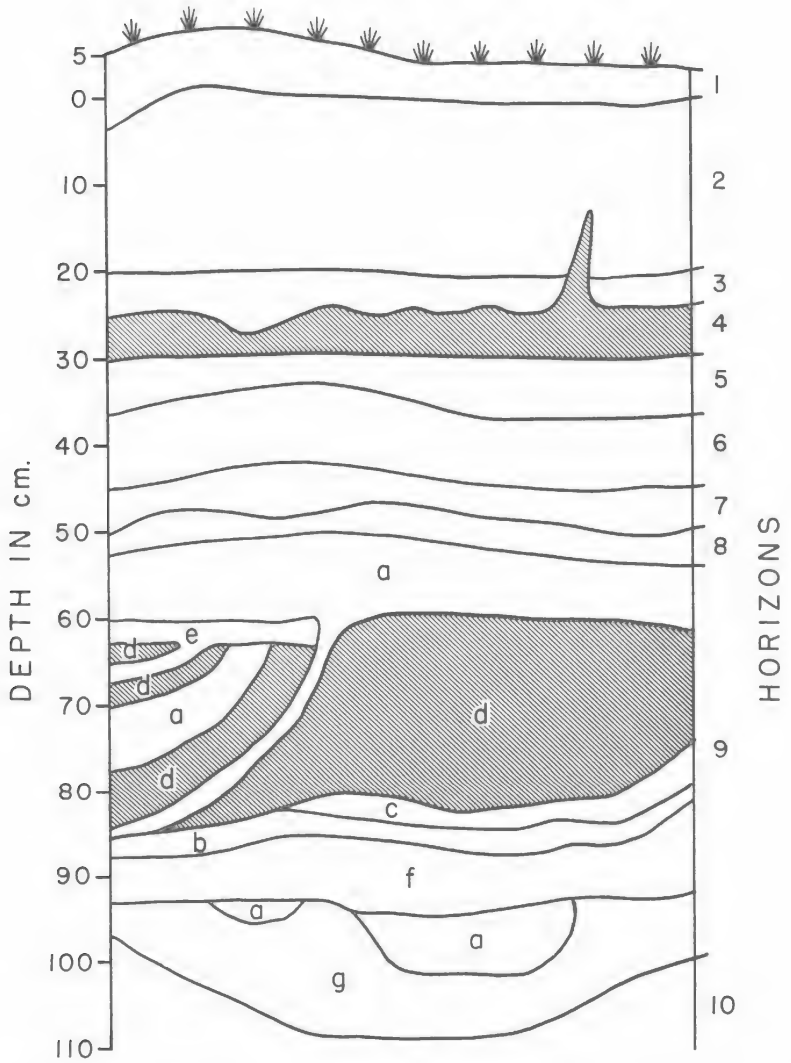

Figure 3. Diagrammatic view of soil profile no. 2. Shaded horizons are composed of volcanic ash; buried A and B horizons occur below each ash horizon. Complexity of horizon 8 demonstrates results of slumping and solifluction. (Horizontal dimensions not to scale.)

Profile: Depth (in cm.)	Horizon	Description
6-0	1	Decaying grass roots and stems; matted and decaying lichens and mosses.
0-20	2	Black (10YR 2/1) loam; weak medium subangular blocky structure; friable to very friable moist; pH 6.5; clear wavy boundary.
20-26	3	Very dark brown (10YR 2/2) loam (?); weak to moderate medium angular blocky structure; friable moist; pH 6.5; abrupt wavy boundary.
26-29	4	Dark brown (7.5YR 3/2) volcanic ash of loamy sand texture; structureless single grained to weak fine granular structure; loose to very friable moist; pH 6.0; abrupt smooth boundary.
29-35	5	Very dark brown (10YR 2/3) silty clay loam; structureless to weak fine to medium subangular blocky structure which tends toward platy structure; friable moist; pH 6.0; clear wavy boundary.
35-42	6	Very dark brown (10YR 2/2) silty clay loam; weak to moderate medium subangular blocky structure; friable moist; pH 6.5; clear wavy boundary.
42-46	7	Dark brown (10YR 3/3) silty clay loam; structureless to weak fine subangular blocky structure; friable moist; pH 6.5; clear wavy boundary.
46-50	8	Very dark brown (10YR 2/2) silty clay loam (?); structureless to weak fine subangular blocky structure; friable moist; pH 6.5; clear wavy boundary.
50-108	9	pH 6.5.
	a	Very dark brown (10YR 2/2) silt loam.
	b	Dark yellowish brown (10YR 3/4) sandy loam.
	c	Greenish gray (5GY 5/1) and yellowish red (5YR 4/8) clay loam or silty clay loam.
	d	Volcanic ash consisting of dark brown (7.5YR 3/2) silty clay loam with yellowish red (5YR 4/6) mottles.
	e	Dark reddish brown (5YR 3/4) clay loam.
	f	Dark brown (7.5YR 3/2) silt loam (?).
	g	Dark brown (10YR 3/3) silt loam.
108+	10	Argillite lag concentrate overlying glacial till.

The third profile (Figure 4) was dug at the top of the first hill north of the airstrip at Nikolski. The effect of considerable wind erosion and some water erosion in this area is reflected in the simpler profile and absence of a thick layer of till at the base of the profile.

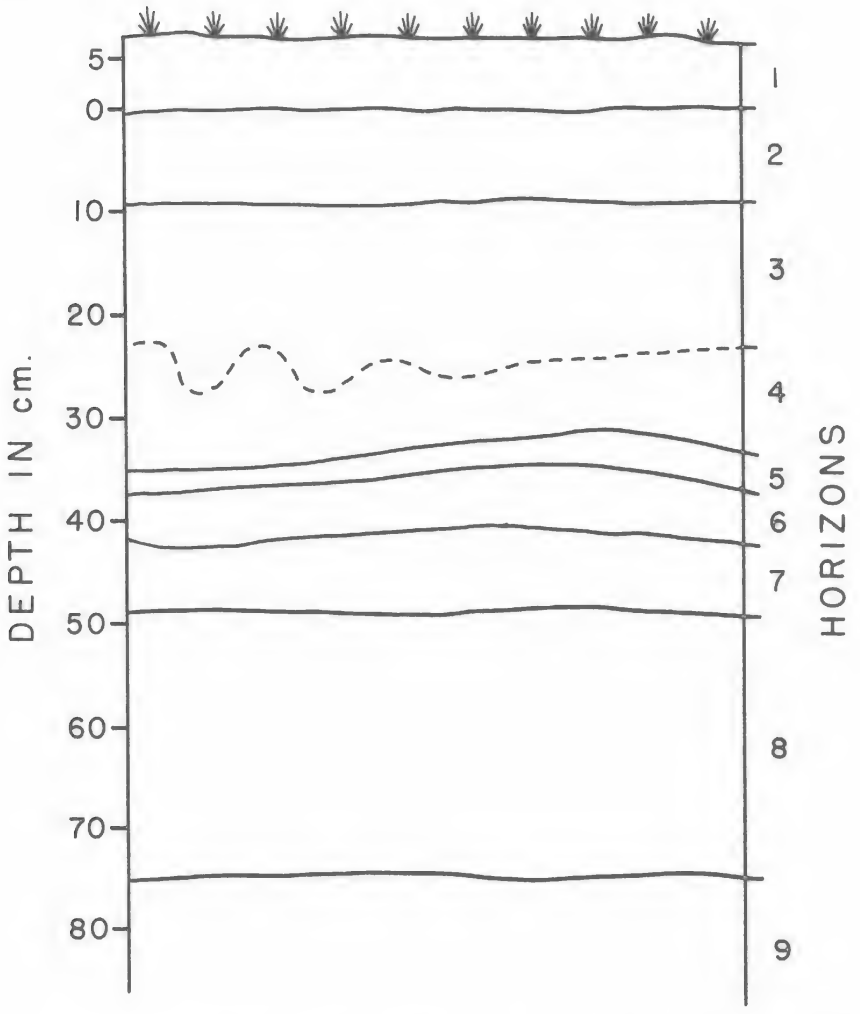

Figure 4. Diagrammatic view of soil profile no. 3. Ash horizons absent due to exposure of site, from which deposited ash would have been blown or washed away. (Horizontal dimensions not to scale.)

Soil Profile Number Three (Figure 4)

Classification: Ando.

Location: About one-half mile north of airstrip.

Description of site: Top of first large hill north of the airstrip (2% slope).

Elevation: Approximately 300 feet.

Climate: Very humid.

Vegetation: Crowberry (*Empetrum nigrum*) heath. Site has been grazed during historic time.

Root distribution: Most roots 0-20 cm., some to 67 cm.

Parent material: Volcanic ash of variable texture and some glacial till over argillite bedrock at 75 cm.

Natural drainage: Well to somewhat excessively drained.

Erosion: Considerable natural erosion; sod still unbroken so probably no accelerated erosion.

Profile:

Depth (in cm.)	Horizon	Description
7-0	1	Mat of slowly decaying crowberry, reindeer moss, and grasses.
0-11	2	Black (10YR 2/1) silt loam; weak medium to coarse subangular blocky structure; firm moist; pH 6.5; gradual wavy boundary.
11-24	3	Very dark brown (10YR 2/2) silty clay loam; weak medium angular blocky which tends toward a weak platy structure; friable moist; pH 6.5; gradual broken boundary.
24-36	4	Very dark brown (10YR 2/1.5) silty clay; weak medium to coarse angular blocky structure; friable moist; pH 6.5; abrupt wavy boundary; many roots in this horizon.
36-38	5	Very dark gray brown (10YR 3/2) silty clay loam; structureless to weak fine to medium subangular blocky structure; friable moist; pH 6.5; abrupt wavy boundary.
38-42	6	Very dark brown (10YR 2/2) loam; weak medium subangular blocky structure; friable moist; pH 6.5; clear wavy boundary.
42-49	7	Dark brown (7.5YR 3/2) loam matrix with small pebbles; weak fine to medium subangular blocky structure; friable moist; pH 6.5; clear wavy boundary.
49-75	8	Large rock fragments.
75+	9	Jointed argillite bedrock with evidences of weathering of the upper surface.

Profiles were also described at points between the three here described. They showed the same over-all pattern but differed in particulars such as depth of various ash layers. From the depths of these marker horizons it would appear that the topography during the time spanned by the last four major ash falls was similar in over-all aspect to that of today, but differing somewhat in detail. The soils described here are the product of long periods during which the slowly decomposing plant materials accumulated; short periods of volcanic activity were interspersed, during which layers of ash were spread generally over the landscape. Variations in this soil sequence can be accounted for adequately on the basis of topographic position.

In the soil profiles studied from the Nikolski region, four major post-glacial ash falls have been noted. These are the apparent equivalent of ash I (Figure 2, horizon 11), ash II (horizon 9a, b), ash III (horizon 5), and ash IV (horizon 3) discussed by Black and Laughlin (1964). Their description of the notable and ancient archaeologic site on the offshore island of Anangula suggests that cultural zone to have occurred between ash II and ash III. Carbon-14 dating of three charcoal samples from this cultural horizon on Aanagula has been reported (*op. cit.*) as follows:

Sample number	Years before the present
I—715	8,425 ± 275
W—1180	7,660 ± 300
I—1046	7,990 ± 230

Ash IV (Figure 2, horizon 3) is estimated by Black to have an age of about 5,000 years. The Chaluka midden at Nikolski, with maximum dated age of about 5,000 years, has resulted from the apparent nearly continuous occupation of the site by resident Aleut populations. This stratified site, exceeding 5 meters in depth, has thus been deposited during the period represented in our natural soil sequence by horizons 1 and 2 (Figure 2).

Acknowledgments

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Construction of Transmitters for Radio-Tracking Hares and Mountain Beavers

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THIS PAPER describes construction, encapsulation, and attachment of miniature radio transmitters for hares and mountain beavers. The circuit is identical to that described by Tester, *et al.* (1964 J. Wildl. Mgmt. 28(1):42-45) but with significant changes in construction methods (Figure 3 shows this circuit). Bureau biologists Paul Martin and Dan L. Campbell contributed valuable suggestions and conducted the field trials leading to the final design.

Materials and Methods

Initial attempts to design a simple slip-on collar or harness transmitter for hares and mountain beavers were discouraging. A hare's neck is considerably smaller than its skull, and a collar of sufficient diameter to slip over its skull and ears was extremely loose. This looseness contributed to skin abrasions and permitted the animal to slip its forefeet through the collar. The neck and skull of the mountain beaver are approximately of the same diameter and hence these animals became very adept at "shucking" the slip-on collar. Harnesses were also tried, but both hares and mountain beavers immediately severed the straps by chewing. These problems were alleviated by designing break-open collars which closely encircled the animal's neck. The final design described here has proved to be satisfactory under field conditions.

Transmitter components, including the antenna, are mounted on a copper-laminated epoxy board (Figure 1) using a printed circuit technique. The board is cleaned with detergent, dried, and the copper surface immediately covered with pressure-sensitive tape to prevent oxidation of the surface to be etched away. The desired circuit/s is then drawn as in Figure 1. The diagonally hatched portion is removed and the board immersed in an etching bath (ferric chloride · hydrochloric acid; commercially available as etching solution from electronic distributors). Etching time varies with temperature but normally requires approximately 30 minutes at room temperature. The board is then washed with tap water, the remaining tape removed, and the board drilled (No. 60 drill) for mounting the components as indicated by the dots in Figure 1.

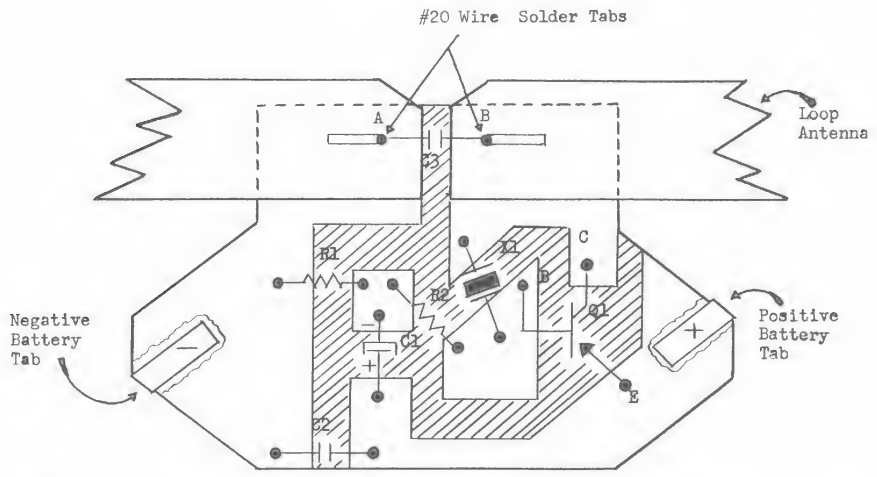

Figure 1. Dorsal view of circuit board with components indicated schematically. X4

The antenna-collar is two strips of soft copper flashing measuring ¼ inch wide, .025 inch thick, and 3 to 4 inches longer than the circumference of the subject animal's neck. The final length (including gap on circuit board) is approximately 4½ inches for hares and 6½ inches for mountain beavers. The two strips are soldered to the circuit board as depicted in Figure 2. It is desirable to drill the antenna and circuit board at points A and B (Figure 1) with a No. 60 drill and solder in 2-inch pieces of No. 20 bare wire to facilitate attaching the tuning capacitor (C_3) when fitting the transmitter to the subject animal.

All components are mounted, using a single-ended style, on the epoxy side of the board and soldered on the copper side (Figure 2). Good soldering techniques, using only rosin core solder, and heat sinking the heat-sensitive components are prime requisites for a suitable transmitter. Attachment sequence is not critical, but heat damage to the transistor can be avoided by mounting that component just prior to final tuning in the laboratory.

Transmitters are assembly-line constructed and initially resonated in the laboratory by using a 50 to 400 micromicrofarad variable capacitor (padder) and the diode detector and milliammeter as described by Verts (1963 J. Wildl. Mgmt. 27(3):325-329). The padder is temporarily soldered in the C_3 position, carefully tuned to resonance, removed and measured on a capacity bridge. Resonance is indicated by a pulsed MA drain and RF field. The range of capacitance is noted for various diameters of the loop as final tuning is conducted in the field.

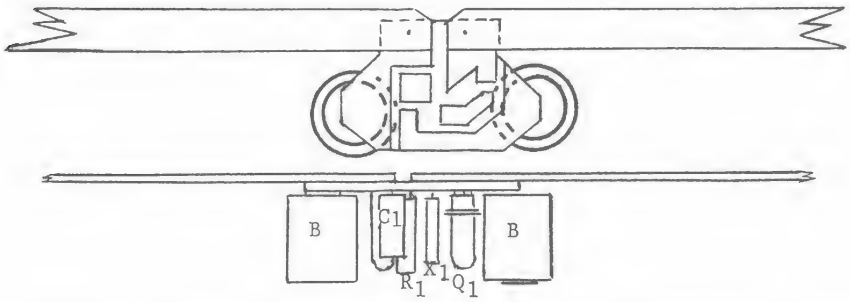

Figure 2. Sketches illustrating single-ended mounting of electronic components and points of antenna attachment. X1

Although it is difficult to obtain a strong signal on these small collars with less than about 1 MA average current drain, this should be attained if possible. Pulse duration, peak pulse current, and repetition time will vary with each transmitter due to component tolerances. For example, a transmitter with two series connected 1.35 volts (V), 350-milliampere-hour (MAH) batteries; a pulse time of 16 milliseconds; repetition time of 750 milliseconds; peak cycle current of 26 MA; and an average current of 0.5 MA will give an expected life of 700 hours or 29 days. This life expectancy can be increased by using four mercury cells in series-parallel, thus increasing the total MAHs available.

The cases of the transistor, electrolytic capacitor, batteries, and the crystal are insulated from each other by wrapping each with one layer of plastic electrical tape. The battery tabs are soldered as indicated in Figure 1 and suspended from the circuit board (Figure 2). A single layer of tape is wrapped completely around the circuit board and components in such a manner that components may be separated from the potting resin. The 2-inch bare wires are left exposed outside the potted transmitter for final field adjustment of C_3. Any light, quick-drying resin or rubber may be used for potting. The potted transmitter should be carefully inspected, since the smallest hole in the resin will permit enough moisture to enter to short out the transmitter.

Field attachment of the transmitter includes careful fitting to the animal's neck, adjustment for a maximum RF field by trial of dipped mica capacitors across the two bare wires, and soldering the antenna (an asbestos strip protects the animal). The excess copper antenna is then cut away, and the attachment is completed by wrapping the collar and tuning capacitor with additional tape. Careful potting around the exposed tuning leads is required to prevent shorting by moisture.

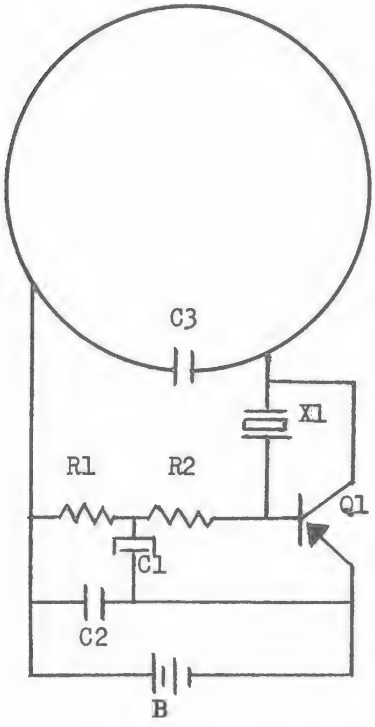

Figure 3. Pulsed transmitter circuit after Tester, *et al.* (1964).

TABLE 1. List of Parts Required for Transmitter Construction

(X_1)	Type HC18/U subminiature crystal
(R_1)	47 K to 470 K, 1/10 W resistor
(R_2)	1 K to 2.2 K, 1/10 W resistor
(C_1)	1 mf to 20 mf, 10 WVDC miniature electrolytic capacitor
(C_2)	.01 mf ceramic disc capacitor
(C_3)	5 mmf to 350 mmf dipped silver mica capacitor
(Q_1)	2N588 or 2N1742 transistor
(B_1)	2, 1.35 V series connected, 350 MAH mercury batteries
	Copper laminated epoxy circuit board, .025-inch thick copper flashing

Results and Discussion

The above-described collar-transmitters have been attached to captive hares for 20 weeks with no indication of abrasion or impairment and have transmitted efficiently for the same period. Final transmitter weight ranges from 30 to 38 grams. A line-of-sight transmission of 10 miles has been attained using a superheterodyne receiver with a calibrated sensitivity of less than 1/10 of a microvolt. Under normal habitat conditions of rolling, forested terrain, signals are attenuated but are ample for tracking both species. At the present time, six free-living hares and mountain beavers are being monitored for acquisition of home-range data.

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Subalpine Fir on Harris Ridge near Hollis, Prince of Wales Island, Alaska

ARLAND S. HARRIS

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Forest Service, U.S. Department of Agriculture
Juneau, Alaska

IN SOUTHEAST Alaska subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.) has been reported at several locations on the mainland. These include: Very Inlet and Boca De Quadra (Taylor, 1929), at the head of Lynn Canal near Skagway (Sudworth, 1908; Anderson, 1919; Hultèn, 1941), at the head of Portland Canal near Hyder (Taylor; Hultèn), and at Taku Glacier (Heusser, 1954). However, to my knowledge, only one occurrence has been observed on any island in southeast Alaska.

Heusser (1960) reported learning through personal communication from Robert A. Gregory, U.S. Forest Service, that subalpine fir had been observed at timberline in the vicinity of Hollis, Prince of Wales Island. This is approximately 80 miles northwest of the nearest previously reported occurrences at Very Inlet and Boca De Quadra (Figure 1). During the summer of 1964 I visited the stand of subalpine fir reported by Gregory to locate the occurrence exactly, to collect specimens for positive identification,[1] and to observe the stand in some detail.

Stand Location and Description

The stand is located at 3,000-feet elevation one mile east of Harris Peak on a ridge (Harris Ridge) between Harris River and Maybeso Creek, approximately three miles southwest of Hollis, Alaska. Subalpine fir occupies a roughly triangular area with apex at the summit of a small peak and extending downslope approximately 300 feet to a maximum base width of 500 feet. Within this area trees occur in scattered clumps on a steep, south-facing alpine meadow above the line of continuous timber (Figure 2). Many clumps consist entirely of fir, while others include mountain hemlock (*Tsuga mertensiana* (Bong.) Carr.) and Sitka spruce (*Picea sitchensis* (Bong.) Carr.). On the summit several small fir trees were found within a clump of mountain hemlock and Sitka spruce. Among the more prominent shrubs

[1] Identification was confirmed by Dr. Elbert L. Little, Jr., U.S. Forest Service dendrologist. Cone and foliage specimens are on file at the U.S. Forest Service Herbarium, Washington, D.C.

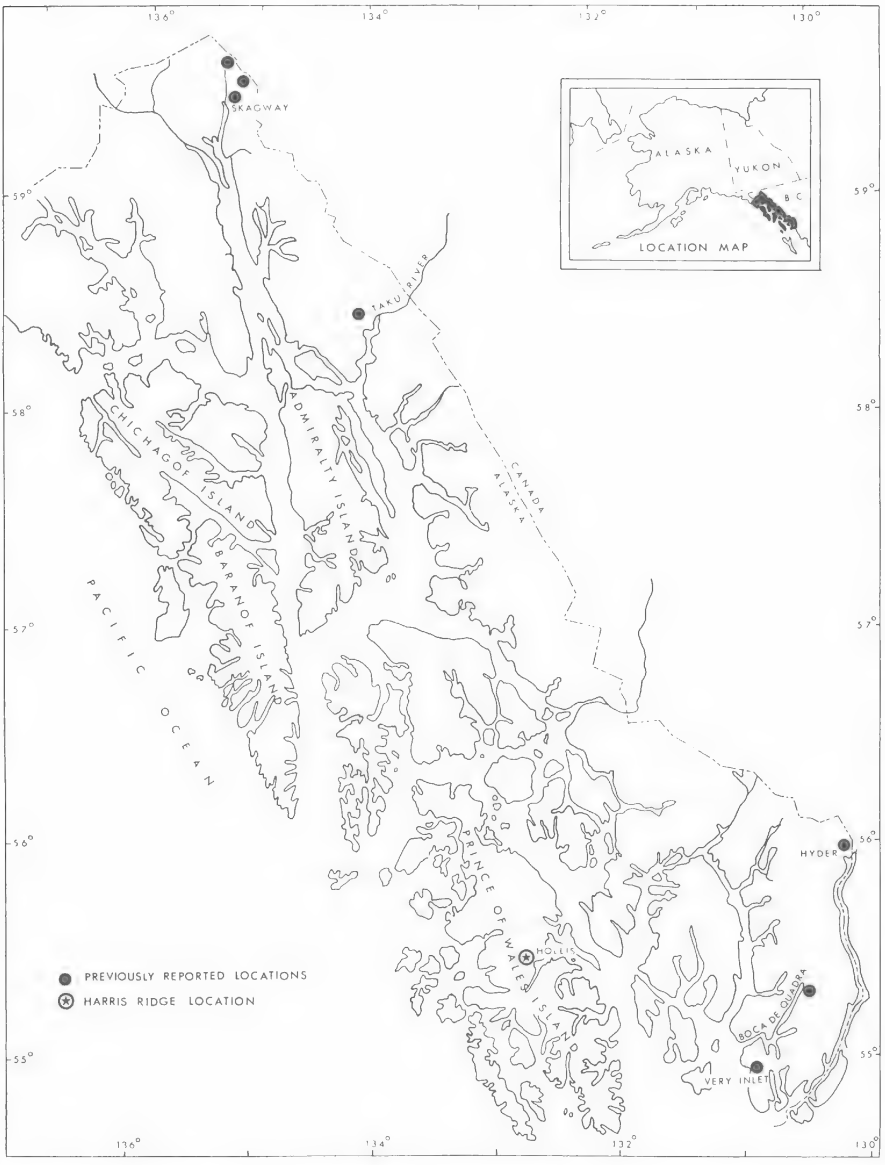

Figure 1. Map of southeast Alaska showing location of subalpine fir on Harris Ridge near Hollis and at other reported locations in southeast Alaska.

Figure 2. Subalpine fir and mountain hemlock on Harris Ridge near Hollis. Trees occur in scattered clumps on a steep alpine meadow.

and herbs present were deer cabbage (*Fauria crista-galli* (Menz.) Makino), bunchberry (*Cornus canadensis* L.), and yellow heather (*Phyllodoce glanduliflora* (Hook.) Cov.).

Best-formed and largest trees were found a short distance downslope, midway within the stand. Tree form ranged from decumbent to erect with much evidence of snow and wind damage. The largest tree measured was 11.0 inches in diameter one foot above ground, 8.6 inches in diameter 4.5 feet above ground, and approximately 17 feet tall. One tree, 3.2 inches in diameter, had 94 growth rings 1.5 feet above ground. A needle rust, tentatively identified as *Melampsorella cerastii* (Pers.) Schroet., was seen on several trees.

Reproduction

Many trees bore cones; those measured averaging 1.5 inches in length. At the time of my visit on September 11, cones were ripe, with some already beginning to disintegrate. All cones examined contained seed, but all seed examined was hollow. Many cones had been damaged by insects, but no insects were seen.

I found no small seedlings. What at first appeared to be seedlings proved to be protruding tips of vine-like decumbent stems overgrown by low alpine vegetation. Reproduction by layering was evidenced by clumped erect stems, several stems sometimes arising from the rooted branches of a prostrate and decaying veteran. Layering of alpine fir has been reported as common by Oosting and Reed (1952), and this appeared to be the principal means of reproduction here.

Plant Geography

The origin of this isolated stand, separated from its closest known neighbor by some 80 miles of low-lying forest and broad fjord, is open to speculation.

Hultèn described subalpine fir as an inland tree whose range reaches Alaska at a few points from the east. Heusser (1954), in reporting the occurrence of subalpine fir on a ridge bordering Taku Glacier, expressed the view that the species presumably spread to Alaska from an unglaciated area or areas in the western Yukon by way of British Columbia during middle postglacial time when major valleys between the Coast and Interior were ice free. However, the presence of this isolated stand on Prince of Wales Island is less readily explained in terms of postglacial migration from the east.

As an alternative, one might speculate that the stand descended from a remnant of the species that survived the last major glaciation. Subalpine fir occurring on Vancouver Island supports this argument. Schmidt (1957) suggested that its distribution on Vancouver Island could be explained to some degree on the basis of survival in mountain-top refugia during one or more glacial periods. However, he could offer no geological evidence that mountains protruded above the ice or that favorable environmental conditions prevailed to allow the species to survive. As circumstantial evidence he cited Dahl's (1946) thesis that, in high mountains bordering a deep ocean, nunataks are bound to exist during major glaciation. This is because a continental ice sheet moving oceanward cannot extend far into deep water for, once afloat, ice is quickly broken up and carried off by the sea. Since the ice surface will maintain a gradual slope back from a relatively low face, high peaks near the sea must protrude above the ice.

Schmidt further pointed to Heusser's report of subalpine fir on a ridge bordering Taku Glacier as evidence that the species can survive under "ice age" conditions.

A similar case could be made to explain the occurrence of subalpine fir on Harris Ridge. Again, there is no direct evidence to support such a conclusion, but, in discussing the glacial history of a part of the Craig C-2 quadrangle, which lies a few miles northeast of the Hollis area, Sainsbury (1961)

suggests that during glaciation some of the mountains to the west which exceed 3,300 feet in height may have stood as nunataks. More convincing proof must await further botanical and geological investigation.

Climate

The Harris Ridge occurrence is noteworthy also in that here subalpine fir, usually considered an inland species, exists under maritime conditions. Six years of precipitation records from sea level near Hollis, at a point approximately three miles from the Harris Ridge location, show an average of 12.6 inches of rain for the three-month period of June, July, and August, and an average annual precipitation of 103 inches. Heusser noted that the distribution of subalpine fir in Alaska at Portland Canal, Taku Valley, and Skagway is coincident with relatively dry areas having a climate more continental than maritime. Schmidt reported that, on Vancouver Island, the climatic stations nearest to known localities of subalpine fir receive less than eight inches of rain during the period of June, July, and August as compared with 10 to 18 inches from stations in the typical oceanic climate. Thus, the occurrence on Harris Ridge suggests that the species is also tolerant to greater precipitation and that precipitation alone is not a major factor in determining its distribution along the coast.

Future Botanical Exploration

Although much botanical exploration has been done in southeast Alaska at lower elevations near tidewater, areas only a few miles inland and at higher elevations remain virtually unexplored. The 1:250,000 U.S. Geological Survey map series compiled in 1952 shows some 30 peaks and ridges at least 3,000 feet in elevation on Prince of Wales Island, some or all of which could presumably offer a suitable habitat for subalpine fir. Thus, it seems unlikely that the island occurrence reported here is unique. Similar habitats can be found on Baranof, Chichagof, Admiralty, and several smaller islands; also, at innumerable locations on the mainland. Until these areas have been systematically searched and the presence or absence of subalpine fir noted, present knowledge of its range in southeast Alaska must be considered incomplete and its postglacial plant geography uncertain.

Summary

Subalpine fir occurs at 3,000-feet elevation on Harris Ridge near Hollis, Prince of Wales Island, southeast Alaska. This is the only occurrence of the species to be reported on any island in southeast Alaska, the nearest reported location being on the mainland approximately 80 miles distant. The origin

of this isolated stand appears more easily explained in terms of descent from a local remnant population that escaped glaciation than from postglacial westward migration.

The occurrence demonstrates that subalpine fir, usually considered an inland tree, is able to grow under maritime climatic conditions and suggests that precipitation alone is not a major factor in its distribution along the coast. More investigation is needed to complete present knowledge of the range and postglacial plant geography of the species in southeast Alaska.

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Soil Temperature and Moisture Regimes in Montana Alpine Soils

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UNIQUE CHEMICAL, morphological, and microbiological features of soils of the alpine have been attributed to low temperatures (Retzer, 1956; Nimlos and McConnell, 1962 and 1965). While this has been generally accepted, the temperature regimes of soils in the alpine have been measured only in Colorado (Marr, 1961). Quantification of the soil-moisture regimes also has received very little study, although it is known that alpine sites vary from well drained to poorly drained (Nimlos and McConnell, 1965).

The objective of this study was to determine the relationship between two environmental factors, soil temperature and moisture, and the distribution of stand-types within the alpine ecosystem.

Literature Review

The flora of the alpine ecosystem in the northern Rocky Mountains has been described by Bamberg (1961), the fauna by Taber and Hoffmann (to be published), and the soils by Retzer (1956) and Nimlos and McConnell (1965). Many of the biotic and soil characteristics are thought to be related to low air and soil temperatures, but the latter have received little actual study. Mean annual soil and air temperatures in the alpine of Colorado (elevation about 12,000 feet) have been shown to be about 26 and 30° F., respectively (Marr, 1961). Mean annual air temperatures have been estimated for the alpine in Montana (elevation about 10,000 feet) at about 30° F. by Nimlos and McConnell (1962), based upon a reduction of 3.5° F. for every increase of 1,000 feet in elevation. Mean annual soil temperatures may be estimated by adding a correction factor to the mean annual air temperature (Smith *et al.,* 1964). According to this procedure, mean annual soil temperatures in the alpine of Montana would be a few degrees more than 32° F. Soil temperatures are particularly significant because of their impact upon the carbon and nitrogen cycles and because of their extensive use as criteria in the new soil classification system (Soil Survey Staff, 1960 and supplement of June, 1964). For instance, the typic subgroups of the "cry" great groups are usually characterized in part by mean annual soil temperatures of less than 32° F.

Soil-moisture gradients occur on many landscapes of the West (McMinn, 1950), but they have never been quantified for the alpine. Nimlos and McConnell (1965) have observed soils in the alpine with contrasting moisture regimes, and Bamberg (1961) has described stand-type (sites) sequences that would also suggest a moisture gradient within the alpine.

Methods

Field. The soil-temperature and moisture regimes of three alpine stand-types on the Beartooth Plateau, about 30 miles southwest of Red Lodge, Montana, were characterized during the summers of 1961, 1962, and 1963. The stand-types are commonly found in the alpine and have contrasting soil-moisture regimes. For purposes of this report they are called fellfield, dry meadow, and sedge-hummock (Bamberg, 1961). The first two are at about 10,500-feet elevation and the third at 10,300 feet. The profile at each of the three sampling locations was described according to standard procedures (Soil Survey Staff, 1951). Detailed morphological, chemical, and mineralogical data necessary for the classification of these soils are available (Nimlos and McConnell, 1965).

The fellfield is on a stony, windswept ridge with a slight slope to the northwest. The soil is a stony phase of the Ptarmigan series: an abbreviated profile description follows:

02 1-0[1] Very dark grayish-brown; tough fibrous, organic, loam turf; abundant,
A1 0-6 Dark brown; stony sandy loam; medium, fine granular; abundant, fine roots.
B21 6-16 Yellowish brown; stony sandy loam; weak, fine granular; common, fine roots.
B22 16-32 Yellowish brown; very stony sandy loam; weak, fine granular; common, fine roots.

The dry meadow occurs near the upper edge of a deep snow-accumulation area on a gentle slope to the east. The soil is a member of the Ptarmigan series.

02 1-0 Very dark grayish-brown; tough, fibrous, organic, loam turf; abundant, fine roots.
A1 0-23 Very dark grayish-brown; gravelly sandy loam; medium, fine granular; abundant, fine roots.
B21 23-38 Dark yellowish brown; gravelly sandy loam; weak, fine granular; common, fine roots.
B22 38-42 Dark yellowish brown; gravelly sandy loam; weak, fine granular; few, fine roots.

The sedge-hummock is in a basin adjacent to a small stream where the water table is very near the surface. The soil is a member of the Vasquez series.

[1] All depths are in inches.

02 4-0 Dark brown; fine sandy loam; coarse platey structure; abundant, fine roots; peaty.
A1 0-8 Dark brown; fine sandy loam, coarse platey structure; abundant, fine roots.
Bg 1 8-12 Dark brown, stained and mottled; sandy loam; single grain structure; abundant, fine roots.
Bg 2 12-16 Dark brown, stained and mottled; gravelly sandy loam; subrounded coarse fragments; single grain structure; common, fine roots.
Bg 3 16-26 Dark brown; gravelly sandy loam; massive structure; few, fine roots.

A seven-day thermograph was placed at each sampling location with the sensing elements at one, six, and 30 inches. The time of installation varied between summers and between locations because of frozen soil and/or snow banks. The soil under deep snow mantles was frozen. The alpine contrasts with lower forested areas in this respect, since the soils in the latter area thaw out under deep snow packs (Phillip Farnes, Soil Conservation Service, Bozeman, Montana). Temperatures obtained with the thermographs were calibrated against a glass thermometer by placing the sensing elements in ice water: the variation was less than 1° F.

Air temperature was determined at the sedge-hummock stand-type with a hygrothermograph housed in a standard Weather Bureau shelter. Precipitation was measured at the same location with a standard rain gauge.

Gravimetric measurement of soil moisture was made by periodic sampling at the two-, four-, eight-, and 18-inch depths. The coarse fragments were removed from each sample. Permanent wilting percentage was determined on the less than 2 mm material with a pressure membrane apparatus (Salinity Laboratory Staff, 1954). The per cent coarse fragments and the bulk densities were determined by removing known volumes from each profile, sieving through a 2 mm screen and weighing the fine and coarse materials. The bulk densities were calculated on the fine material by assuming a specific gravity of 2.65 for the coarse fragments and calculating their volume. The difference between the pit volume and the volume of coarse fragments was taken as the volume of the fine material.

Calculations. Mean soil and air temperatures were calculated from daily maxima and minima.

The procedure for calculating available water was essentially that outlined by Reinhart (1961). Inches of soil water in each layer (0-2, 2-4, etc.) were calculated by converting the measured gravimetric moisture percentage to the volumetric and multiplying times the effective depth. The effective depth was the layer's thickness corrected for coarse fragments. Only the depths with abundant or common roots (taken from the profile description)

were included in the calculations: 32, 38, and 20 inches for the fellfield, dry meadow, and sedge-hummock stand-types, respectively.

Inches of available water were obtained by subtracting the inches of water at permanent wilting percentage from the water content in each layer. The sum of the inches of available water in each layer with abundant or common roots represents the inches of water available for plant growth.

Results

Temperature. Maximum air temperatures were generally in the fifties and sixties and minima were in the low thirties. The maximum air temperature measured during the three years was 72° F.; the minimum was 12° F.

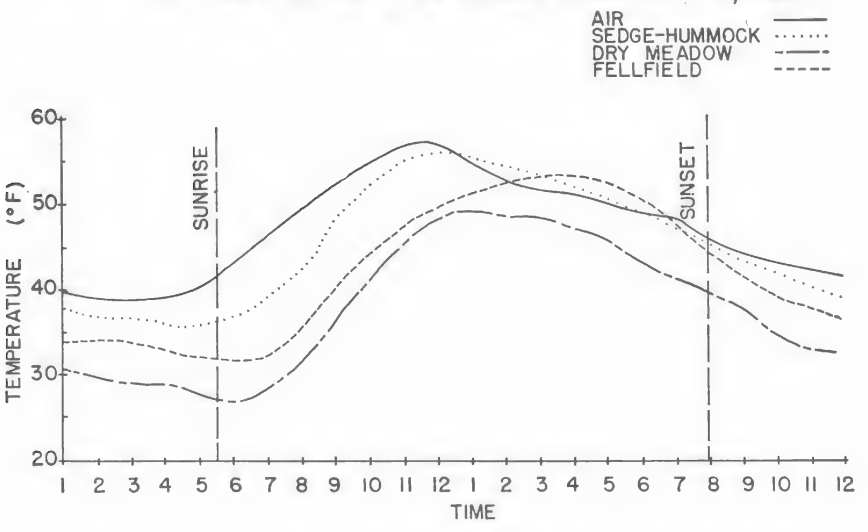
Soil temperatures decreased with depth and were lowest in the very wet (sedge-hummock) stand-type. At the one-inch depth they closely resembled the air temperatures. The maximum soil temperatures measured during three years were at the one-inch depth and were 67, 68, and 66° F. in the fellfield, dry meadow, and sedge-hummock, respectively. The maximum temperatures at the 30-inch depth seldom rose above 45° F.

TABLE 1. Mean Temperatures of the Air and of Soils in Three Alpine Stand-Types during the Summers of 1961, 1962, and 1963

Stand-type	*Depth (in.)*	*1961* °F.	*Dates*	*1962* °F.	*Dates*	*1963* °F.	*Dates*
Fellfield	1	39		43		43	
	6	40	7/2-9/9	42	6/23-8/22	39	6/20-9/20
	30	38		35		34	
Dry meadow	1	38		42			
	6	39	7/2-9/9	39	7/21-8/22		
	30	40		33			
Sedge-hummock	1	43		36		37	
	6	36	7/2-9/9	34	7/8-8/22	35	6/20-9/20
	30	30		27		28	
Air (sedge-hummock)		47	7/15-9/12	45	7/14-8/15	46	7/12-9/21

Mean air and soil temperatures for the various periods of measurement are shown in Table 1. The 1963 data on the dry meadow were discarded because of a mechanical error in the thermograph. Assuming that the periods of measurement roughly approximate the summer, the summer air temperatures in the alpine average about 45° F. Long-term mean air temperature

FIGURE 1. AVERAGE DAILY MARCH OF AIR AND SOIL TEMPERATURE (AT ONE INCH) IN THREE ALPINE SITES DURING AUGUST 6 TO 12, 1961.



for July and August at Red Lodge, Montana (elevation 5,575 feet), is 64° F. and at Billings, Montana (elevation 3,567 feet), it is 72° F. (Weather Bureau, 1961). Thus the summer temperatures in the Beartooth alpine ecosystem are 20 to 30° F. cooler than at low-elevation stations.

The mean soil temperatures generally decrease with depth, although in two instances the means were nearly constant throughout the profile. The means do not vary appreciably between the fellfield and dry meadow, but the sedge-hummock (Vasquez soil) is generally a few degrees cooler. This is undoubtedly due to the saturated condition of the soil (Fitton and Brooks, 1931).

The daily fluctuation of air temperature and soil temperature at the one-inch depth of each stand-type (sites) for a representative period is shown in Figure 1. The shape of the curve is approximately the same as that shown by Smith *et al.* (1964) for soil-temperature fluctuations at low elevations. Temperature ranges for both air and soil at the one-inch depth over this period are about 20° F., which is much less than has been observed at lower elevations (Bliss, 1944; Fitton and Brooks, 1931; and Smith *et al.,* 1964). The fluctuation decreased with depth to about 6° F. at the six-inch depth and about 2° F. at the 30-inch depth.

At each depth the mean daily range of soil temperature over the summer was largest at the dry meadow and least at the sedge-hummock.

TABLE 2. BULK DENSITIES, PER CENT COARSE FRAGMENTS, AND PERMANENT WILTING PERCENTAGE OF THE SOIL IN THE THREE STAND-TYPES

Stand-types	*Depth (in.)*	*Bulk Density*[1] *(gm./cc.)*	*Coarse Fragments (%)*	*Permanent Wilting Percentage*
Fellfield	0-2	0.8	47	36
	2-4	0.8	47	17
	4-8	0.8	47	10
	8-20	0.9	57	8
Dry meadow	0-2	1.5	49	19
	2-4	1.5	49	7
	4-8	1.5	49	7
	8-38	1.5	49	4
Sedge-hummock	0-2	0.9	1	49
	2-4	0.9	1	28
	4-8	0.9	1	28
	8-18	1.2	8	9

[1] Density of the material less than 2 mm in diameter.

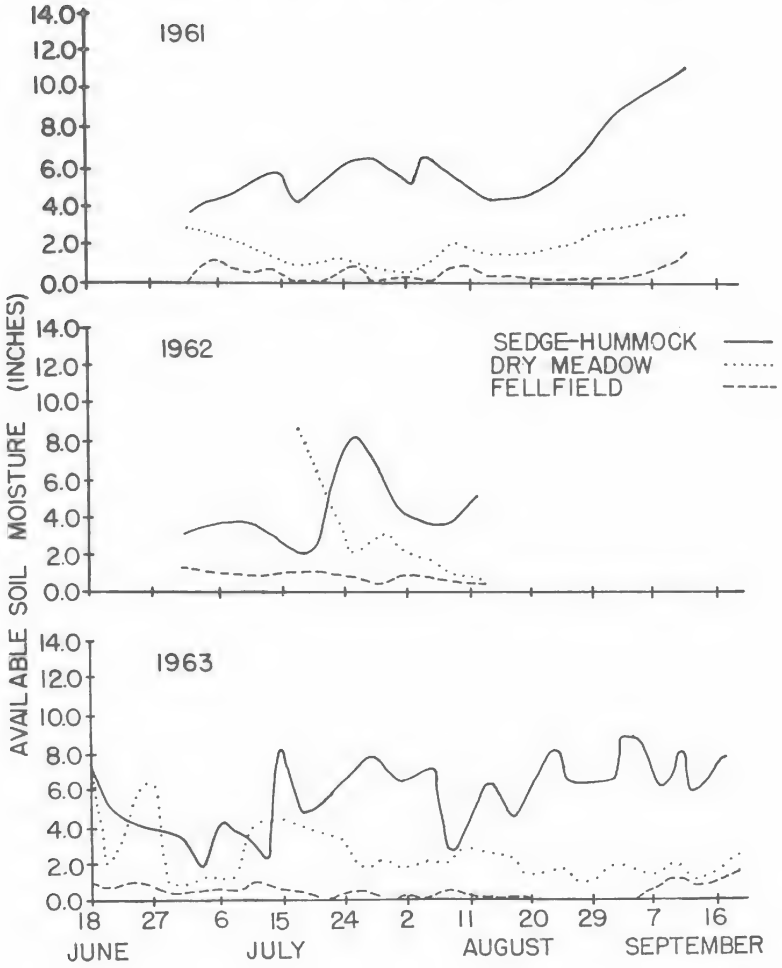
Moisture. The bulk densities, per cent coarse fragments, and permanent wilting percentages of the various horizons are given in Table 2. The dry meadow profile was sampled once; the others twice. It is not known why the bulk density is so high in the dry meadow profile.

Available moisture in each of the three stand-types (sites) is presented in Figure 2. The collection of moisture data for the dry meadow was delayed in 1962 because the soil was frozen and covered by a deep snow pack until July 18.

The three stand-types are ordinated along a soil-moisture gradient with the sedge-hummock the wettest, the fellfield the driest, and the dry meadow intermediate. Moisture is available for plant growth during the entire summer at the sedge-hummock and dry meadow. But the fellfield has only limited moisture, and this may inhibit plant growth.

Precipitation at the sedge-hummock was 7.7 inches from June 18 to September 12, 1961, 5.4 inches from June 12 to August 22, 1962, and 6.0 inches from June 14 to September 22, 1963. Thus the alpine ecosystem on the Beartooth Plateau receives considerable summer precipitation.

FIGURE 2 SEASONAL MARCH OF AVAILABLE SOIL MOISTURE IN THREE ALPINE SITES



Discussion

Temperature. Data have been collected on one alpine area, the Beartooth Plateau, to help characterize the environment of the alpine ecosystem in western Montana. The data support the general observation that the alpine ecosystem is a cold environment. Mean summer air temperatures are about 45° F., or 20 to 30° cooler than grasslands at low elevations, and below-freezing temperatures may occur at any time. Mean summer soil tem-

peratures were 42, 40, and 34° F. at the one-, six-, and 30-inch depths, respectively, in the well-drained soils (fellfield and dry meadow) with slightly lower values in the sedge-hummock. A mean summer soil temperature of less than 40° F., at the 20-inch depth, is suggested as a criterion for soil classification.

Assuming the above estimates, valid characterization of soils in the alpine of Montana could be made with mean annual soil temperatures of 35° F. or less and mean summer soil temperatures of 45° F. or less. Thus the 32° F. mean annual soil temperature that is currently being used to characterize in part the typic subgroups of some "cry" great groups should be raised a few degrees.

The daily temperature fluctuations in the alpine are much less than those that occur at lower elevations even though the solar radiation is very large at high elevations (Gates, 1963).

Perhaps the most interesting use of temperature data can be made in the interpretation of their impact upon the nitrogen cycle. Soils of the alpine in Montana (Nimlos and McConnell, 1965) and at other cold sites (Jenny, 1941) have been shown to contain large amounts of total nitrogen; from five to ten times more than many grassland soils. Yet even with these large supplies of total nitrogen, the supplies of ammonium and nitrate are very low (R. Faust, unpublished data). This is due at least in part to the influence of low temperatures on the microbial populations. The number of microorganisms is less than 1 per cent of those in warmer soils (Faust and Nimlos, 1965). Autotrophic nitrifying bacteria are absent from soils of the arctic (Boyd, 1958), soils that are morphologically similar to soils found in the alpine. Thus nitrogen in soils of the alpine is concentrated in the organic form and is unavailable to plants.

Moisture. The soil-moisture data have certain limitations because of the assumptions upon which the calculations were based: that moisture uptake from horizons with only a few roots is minimal; that the specific gravity of the coarse fragments is 2.65; and that the 15 atmosphere tension represents the lower limit of moisture availability.

The poorly drained soils of the sedge-hummock are never deficient in available moisture and in this respect are similar to other soils at lower elevations with impeded drainage. The well-drained soils of the dry meadow also have sufficient moisture available during the growing season. The well-drained soils of the fellfield apparently have some short periods of moisture deficiency. Only at this stand-type is plant growth likely to be limited by available moisture.

The three stand-types are ordinated along a gradient of available soil moisture from very dry to very wet, which indicates that soil moisture is the environmental factor primarily responsible for their distribution. Since the alpine ecosystem occurs on a wide range of moisture regimes, some environmental factors other than soil moisture are responsible for the occurrence of this ecosystem. Apparently those other factors are low temperatures and/or wind damage.

Summary

Soil-temperature and moisture regimes for summer periods are characterized at three stand-types commonly found in the alpine ecosystem of Montana. The stand-types are uniformly cold, and their distribution is apparently not determined by soil temperatures. The mean summer air temperatures are about 45° F., and the mean summer soil temperatures are about the same in the surface horizon of the well-drained soils. The poorly drained soils are a few degrees cooler than the well-drained ones at comparable depths.

Suggested criteria for the characterization of soils of the alpine are less than 35° F. for mean annual and less than 40° F. for mean summer soil temperatures. These low temperatures apparently account for the low microbial populations, weak profile development, accumulation of organic matter, and low nitrate and ammonium contents in alpine soils.

The moisture regimes of the stand-types vary from those with summer-moisture deficiencies to those with a moisture surplus. The three stand-types, fellfield, dry meadow, and sedge-hummock, represent points ordinated along a moisture gradient from dry to wet. Apparently available soil moisture is the dominant environmental factor determining the distribution of the stand-types.

Acknowledgement

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Some Aspects of the Ecology of Hydroids off the Oregon Coast[1]

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CERTAIN HYDROIDS may serve as indicators of bottom conditions since the sessile polyp stages are dependent on conditions present in their own area (temperature, salinity, bottom type, nutrients, food, predators, etc.). Hydroids apparently are chiefly carnivorous (Hyman, 1940). Thus, factors affecting primary production affect hydroids indirectly through their food supply (zooplankton, eggs, larvae, etc.).

Hydroids are important fouling organisms. Ayers and Turner (1952) reported that 265 of the known 2,000-3,000 species have this property. *Eudendrium, Tubularia, Clytia, Obelia,* and *Plumularia* were among those implicated. A square foot of surface may support several pounds of hydroid fouling (Ayers and Turner, 1952).

Little is known about the bathymetric distribution of hydroids. Fraser has discussed some bathymetric ranges of genera and species (1937, 1946). Nutting (1904) pointed out that gaps in the known distribution of hydroid species bathymetrically are more likely due to incomplete exploration than to discontinuous distribution with depth.

Fraser (1911, 1925, 1937, 1946, 1948) studied hydroid distributional patterns from the Northeast Pacific to Peru, and from some of the oceanic islands. Depths were recorded in Fraser's *Hydroids of the Pacific Coast of Canada and the United States* (1937) and in most of his reports shortly before this, but other papers on Pacific Coast hydroids have generally been deficient in bathymetrical information. Fraser's study included intertidal forms and only a few deeper ones. This present study includes only subtidal forms. Some species found during this study were not mentioned by Fraser. He (1937) implied collections off Oregon near Heceta Head and Yaquina Point in water deeper than 60 fathoms (probably some of the *Albatross* collections) but did not specify when they were made.

Before 1937 few shore collections of hydroids had been made between Cape Flattery, Washington, and San Francisco Bay, California; very few col-

[1] This report includes part of the author's master's thesis presented at Oregon State University.

lections from deeper stations had been examined (Fraser, 1937). The *Albatross* (Townsend, 1901) collected off Oregon in 1888 and 1889 in water 20 to 277 fathoms (36.6 to 506.6 meters) deep; only one station, however, was deeper than 200 meters. Late in 1890, collections were made at depths of 759, 786, and 345 fathoms (1,388, 1,437, and 631 meters).

Fraser (1948) reported ". . . in July and August, 1942, the Coos Bay region of the Oregon coast was investigated to some extent." This work was apparently done by the Allan Hancock Foundation, and the results were incorporated in Fraser's 1948 work. Evidently no other collection has been done off Oregon.

Among the hydroid families the Campanularidae are predominantly shallow water forms (Nutting, 1915); the Plumularidae extend over a wide depth range (Nutting, 1900); and the Sertularidae are intermediate in distribution (Nutting, 1904). The greatest numbers of species tend to be concentrated in shallower water; this fact is probably related to environmental variation in the euphotic zone with its good food supply, and to suitable solid substrate.

Most hydroid species known live in shallower water, but some have been reported from abyssal and hadal depths. Zenkevitch and Birsten (1956) reported that 0.4 per cent of hydroid species occur in depths of more than 4,000 meters, and 0.2 per cent in more than 5,000 meters. Kramp (1956) described *Halisiphonia galatheae* from 8,210-8,300 meters in the Kermadec Trench. This is the greatest known depth for hydroids.

Allman (1871, 1872) reported hydroids growing epizoically on British snails: *Heterocordyle conybearei* on the snail *Buccinium, Eudendrium ramosum* on an oyster shell, and *Hydractinia echinata* on a *Buccinium* shell occupied by a hermit crab. He did not, however, go into any detail about the relationships.

Dales (1957) stated that "On the surf-swept beaches of Southern California, the wave action does not usually permit the growth of delicate hydroids on exposed surfaces in the intertidal zone. *Clytia bakeri,* however, may be found growing on the tip of the shells of the small clam *Donax gouldi* as well as on the larger Pismo clam (*Tivela stultorum*), or more occasionally on the spire of the olive shell (*Olivella*). . . . A similar association between a hydroid and *Donax* occurs on the Gulf coast of the United States. The hydroids probably benefit from their position near the feeding currents of the clam, while in the case with *Olivella* the hydroid gains mobility, and its usual position near the siphon may further improve the chances for food."

Symbiotic relationships of hydroids off Oregon have not been widely studied.

Materials and Methods

Hydroid specimens were collected during the years 1960-1964 from the R/V ACONA and fishing boats with a biological dredge, an anchor dredge, or an otter trawl. Hydroids are usually found on hard substrates, but technical problems have caused us to avoid rocky areas for most of the collections. The anchor dredge used does not function well in rocks, and nets are easily torn. The biological dredge was found to work better in rocky areas. Thus, most of the thecate hydroids were collected by this method.

Anchor-dredge samples were strained through a fine-mesh screen on board the vessel to separate the organisms from the sediment and preserved (generally in formalin) on the vessel. (Mesh size of the screens used was 0.297 or 0.420 mm opening.)

Otter-trawl and biological-dredge samples were rough-sorted on board and re-sorted to taxonomic groups in the shore laboratory.

Discussion

The hydroids collected and their bathymetric occurrences are shown in Table 1. A summary of the bathymetric and geographical distribution of the hydroids found during this study is presented in Table 2. Most species occur in shallow water, but one notes a rapid decrease in number of species with depth. That 35 per cent of the species are restricted to the upper 100 meters indicates that light may play a significant role in determining their distribution. Also, the variety of habitats afforded in the coastal zone may provide more ecological niches.

Only one species (*Lafoea fruticosa,* from 1,829 meters) is shown to occur on a mud bottom (see Table 1). This species was also taken from 64 meters on an unknown bottom type. Four species were found on a sandy bottom: *Hydractinia* sp., epizoic on the snails *Mohnia freilei* and *Olivella biplicata; Perigonimus repens,* epizoic on the pelycepod *Acila casternsis; Plumularia alicia,* on a mat-like substrate possibly of compacted detritus; and *Aglaophenia diegensis,* possibly attached to an isolated rock or shell. Four species (*Aglaophenia* sp., *A. diegensis, Campanularia* sp., and *Sertullarella turgida*) were found on a rocky bottom. The bottom types for the other species were not determined.

A. G. Carey of Oregon State University has surveyed particle size of sediments in the region (Carey, 1965), and there appears to be no correlation

between the particle size and the hydroids present. However, substrate information is available for only a few areas covered.

Some host specificity occurs among the hydroids epizoic on other animals. *Egmundella gracilis* was found only on *Neptunia lyrata*. *Clava* sp. was found only on *Mohnia freilei* and *Lafoea gracillima* only on certain tube worm tubes. *Hydractinia* spp., on the other hand, were found on a variety of hosts. How-

TABLE 1. BATHYMETRIC DISTRIBUTION OF HYDROIDS COLLECTED OFF OREGON

	Depth in Meters																				
Species	*0- 99*	*100- 199*	*200- 299*	*300- 399*	*400- 499*	*500- 599*	*600- 699*	*700- 799*	*800- 899*	*900- 999*	*1000-1099*	*1100-1199*	*1200-1299*	*1300-1399*	*1400-1499*	*1500-1599*	*1600-1699*	*1700-1799*	*1800-1899*	*1900-1999*	*2000-2099*
Abietinaria anguina	R	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Acryptolaria sp.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanularia sp. ?	R	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Halecium sp.	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Halecium corrugatum	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Lafoea adnata	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Abietinaria abietina	X	S	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aglaophenia diegensis	R	R	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aglaophenia inconspicua	X	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Sertularella turgida	X	R	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plumularia alicia	S	O	O	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Abietinaria traski	X	O	O	O	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Aglaophenia sp.	R	R	O	O	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eudendrium tenellum	X	O	O	O	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hydrallmania distans	X	O	O	X	X	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Campanularia verticillata	X	X	O	O	O	O	O	O	X	.	.	.	.	.	.	.	.	.	.	.	.
Egmundella gracilis	X	O	O	O	O	O	O	O	E	.	.	.	.	.	.	.	.	.	.	.	.
Lafoea dumosa	X	O	O	O	O	O	O	O	X	.	.	.	.	.	.	.	.	.	.	.	.
Lafoea gracillima	X	O	O	O	E	O	O	O	O	X	.	.	.	.	.	.	.	.	.	.	.
Perigonimus repens	E	E	E	E	E	O	O	O	O	E	.	.	.	.	.	.	.	.	.	.	.
Lafoea fruticosa	X	O	O	O	O	O	O	O	O	X	O	O	O	O	O	O	O	O	M	.	.
Hydractinia sp.*	E	O	O	E	O	E	E	E	E	E	E	E	O	O	O	O	O	O	O	O	E
Campanularia sp.	.	.	.	.	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Obelia sp. ?	.	.	.	.	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Clava sp.	.	.	.	.	.	E	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.

M = muddy bottom. E = epizoic (bottom type not given for these).
S = sandy bottom. X = unknown bottom type and substrate.
R = rocky bottom. O = presumed occurrence.

* May represent several species.

TABLE 2. DISTRIBUTION

Name	*Geographic Range (Eastern Pacific)*	*Bathymetric Range (meters)*
Clava sp.	44° 38.8′N, 124° 53.9′W	100-1600
****Perigonimus repens* (Wright)	Admiralty Islands, Lynn Canal, Alaska to Santa Elena Bay, Ecuador, and the Galapagos	16-914*
****Eudendrium tenellum* Allman	Summer Strait, Alaska, to Gorgona Island, Colombia	0-479
Hydractinia sp.	44° 17.3′N, 44° 39.1′N	25-731
Campanularia (?) sp.	44° 39.7′N, 124° 04.5′W	10
****C. verticillata* (Linn.)	Bering Sea to San Diego, California and Chile	13-869
Obelia (?) sp.	44° 38.8′N, 124° 51.8′W	400
****Egmundella gracilis* Stechow	Rose Harbour, Queen Charlotte Islands to San Francisco Bay, California	13-800*
Halecium spp.	43° 59.8′N, 124° 51.6′W	400
****H. corrugatum* Nutting	Lynn Canal, Alaska to Santa Maria Bay, Lower California	0-110
Acryptolaria sp.	44° 17.2′N, 124° 39.8′W	77
****Lafoea adnata* Fraser	Near Farallon Islands, California to 43° 59.8′N*	60-92*
****L. dumosa* (Fleming)	Bering Sea to Isla Partida, Gulf of California	9-823
****L. fruticosa* (M. Sars)	Bering Sea to San Francisco Bay, California	6-1829?*
****L. gracillima* (Alder)	Bering Sea to Northern Ecuador	6-957
****Abietinaria abietina* (Linn.)	Bering Sea to San Diego, California	0-146
A. anguina (Trask)	Masset, Queen Charlotte Islands to San Quintin Bay, Baja, California	0-64
A. traski (Torrey)	Berg Inlet, Alaska, to San Diego, California	9-400*
****Hydrallmania distans* Nutting	Queen Charlotte Islands to San Diego, California	6-400*
Sertularella turgida (Trask)	North end of Graham Island, Queen Charlotte Islands, to Santa Maria Bay, Baja, California	0-200*
Aglaophenia sp.	44° 39.7′N, 43° 55.4′N	10-400

TABLE 2 (CONTINUED)

****A. diegensis* Torrey	44° 39.7′N* to Santa Maria Bay, Baja, California	0-110*
A. inconspicua Torrey	44° 17.2′N* to Santa Maria Bay, Baja, California	0-154
Plumularia alicia Torrey	44° 39.7′N* to South Bay, Cerros Island, Baja, California	0-329

* Range extended by this report.
** Not previously reported from Oregon waters.

ever, it could not be determined whether all *Hydractinia* were the same species, since reproductive structures were generally missing. *Perigonimus repens* was found concentrated on the shell in the area of the incurrent siphon of 74 per cent of *Acila castrensis,* and on the opercula of *Colus halli.* However, it was not localized on the shells of *Nassarius fossatus.*

Host specificity is probably related to the desirability of the host surface as a suitable place for settling and growth, and to habits of the host which place the hydroid in a position where it can get food (zooplankton and possibly drifting or settling organic detritus). Perhaps *Acila castrensis* and *Colus halli* burrow more than *Nassarius fossatus,* and *P. repens* is eroded away from all but the protected parts of the surface, or else the location is advantageous for feeding.

Some hydroids served as host to epizoic animals (Table 3), but the small numbers of examples do not permit judgments of host specificity.

Summary and Conclusion

Twenty-six species of hydroids were collected off the Oregon coast. Seventeen of these were identified to species, the rest to genus. This is the first report from Oregon waters for 12 species. Bathymetric ranges were extended for four species.

Five hydroid species were found growing epizoically on mollusk shells; six were found growing on other hydroids. *Hydrallmania distans, Abietinaria* sp., and *Sertularella turgida* served as hosts to other hydroids.

The number of species decreases rapidly with depth. Nearshore species are probably regulated to some extent by water aeration, food supply (related to light), and substrate; deeper-water species appear to be regulated by pressure and substrate.

The host organisms always come earlier in ecological succession than those epizoic on them. The epizoic forms depend on a suitable substrate. They may be found on the host because it offers advantageous position for feeding

TABLE 3. ANIMALS EPIZOIC ON HYDROIDS

	Hosts									
Epizoons	*Abietinaria abietina*	*Abietinaria anguina*	*Acryptolaria sp.*	*Aglaophenia* sp.	*Aglaophenia inconspicua*	*Halecium* sp.	*Hydrallmania distans*	*Lafoea dumosa*	*Lafoea gracillima*	*Sertularella turgida*
Cibicides lobatulus?			○		○			○	○	
Cibicides labatulus	○					○				○
Discorbis columbiensis			○							
Demospongiae	●		●	●	●			●		●
Skeneopsis sp.?	△		△							△
Laginipora sp.	▲									
Myriozoum coarctatum				▲						
Campanularia sp.?		□								
Campanularia sp.							□		□	
Eudendrium tenellum							□			
Halecium corrugatum	□									
Lafoea adnata	□									□
Lafoea gracillima							□			
Obelia sp.?							□			

Animals on hydroids: foraminiferans ○, sponge ●, mollusks △, bryozoans ▲, hydroids □.

or circulation. It may be that the host merely provides a suitable, hard substrate, and the epizoic relationship may be fortuitous.

Hydroids on mollusks apparently are somewhat host specific. They may reflect the nature of the host surface and the habits of the host.

Acknowledgements

Appreciation is expressed to Dr. James E. McCauley of the Department of Oceanography for suggesting the problem, for placing his facilities at Oregon State University at my disposal, for identifying the Mollusca, and for

helpful suggestions and criticism. Thanks are also due Dr. Gerald A. Fowler who identified the foraminiferans.

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Erratum

In Dodge, W. E. and M. Boyd Church. 1965. Construction of transmitters for radio-tracking hares and mountain beavers. N.W. Sci., 39(3): 118-122, battery polarity is incorrectly indicated in Figure 3. Please reverse polarity to indicate positive voltage to the emitter.

Habits and Life History of the Bronze Flea Beetle, Altica tombacina (Mannerheim) (Coleoptera - Chrysomelidae)

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IN THE summer of 1959 during an ecological study on Saddleback Mountain in the Oregon Coast Range in Northwestern Oregon, a bronze flea beetle, which proved to be *Altica tombacina* (Mannerheim), was found feeding extensively on the fireweed plant, *Epilobium angustifolium* L. Correspondence with Dr. Louis G. Gentner, a recognized authority on the genus *Altica,* concerning identification of the beetle disclosed that very little was known about the life history or habits of this species. Furthermore, Dr. Gentner stated that though he had examined many specimens he had never found a male and that the external characteristics by which males had been designated by Horn (1889) apparently were not valid for this species. He also mentioned the possibility of parthenogenetic reproduction.

As the lack of information about the bronze flea beetle presented a challenge, certain members of the Linfield research group began, as time permitted, observations and experiments which led ultimately to fairly complete knowledge concerning its life history.

Materials and Methods

Several groups of larvae were collected from fireweed plants in the fall of 1959 and taken to the Biology Department of Linfield College where they were placed in glass rearing cages with fine-mesh covers. There they were supplied from time to time with fresh fireweed leaves for food and were observed to pupate on the bottoms of the cages. From these larvae more than 30 adult bronze flea beetles were obtained, definitely establishing the identity of the larvae and giving preliminary data regarding length of stages in the life cycle.

On August 20, 1960, a series of fairly mature larvae was collected for further observation. These were placed in rearing cages in the laboratory and were found to have pupated on August 30. From 10 of them the data were obtained for Table 3 on the metamorphosis from pupa to adult during the last two days of pupation.

On May 13, 1961, one beetle was isolated from several collected on Saddleback Mountain that day. She was placed on a fresh fireweed leaf in a small cage in the laboratory. Throughout the summer and until September 20, this beetle, together with others reared from eggs produced by her, was checked at frequent intervals. All beetles under observation were supplied with fresh fireweed leaves as needed. It was possible to keep the leaves fresh and turgid for several days by removing them from the stem of the plant and placing the basal end of the leaf in loosely corked, small glass vials filled with water. This technique also kept the beetles from getting into the water and drowning. Excepting the technical description of the adult and the data in Table 3, nearly all of the following observations and records on the life history of *Altica tombacina* are from this female and her laboratory-reared progeny.

Life History

Taxonomy of Adult. Altica tombacina was first described by Graf-Carl G. Mannerheim in August, 1853, from a single specimen taken from herbage along a small creek on the Tschunuktnu Peninsula, Kenai, Alaska. It belongs to the family Chrysomelidae, most members of which are called flower or leaf beetles, but the adults of the subfamily Alticinae jump like fleas and for this reason are termed flea beetles. In some books the genus is spelled *Haltica.*

The external sex characteristics of the genus *Altica* are described by Dr. Gentner (pers. comm.) as follows:

> Normally males have the first joint of the anterior tarsi larger and broader than in the females, and the last ventral segment of the abdomen is sinuate on each side with a rather noticeable median lobe, more or less concave and smooth, with a longitudinal or triangular median impression extending three-fourths to two-thirds the length of the segment. In the female the last ventral segment is usually convex without a median impression.

Dr. Gentner, who has specimens in his collection from Oregon, Washington, British Columbia, Alberta, and Alaska, has never found the enlarged or broadened first joint of the anterior tarsi. He did find some specimens having the ventral median indentation, giving the impression that they might be males. But when dissected they proved to be females.

Description of Life Stages. The cylindrical, finely punctate eggs, 0.6 mm long by 0.3 mm wide, are yellow and are deposited on undersurfaces of leaves (Figure 1).

The tiny, newly hatched larvae, 1.5-2.0 mm in length, have pale-yellow bodies with four dark dots on the dorsal side, their heads varying from yellow

to black (Figure 2). The body soon darkens, with the head, legs, spots around hairs, and thorax becoming black until the entire animal is a uniform shiny black in or before the end of the third, and last, instar when it measures seven mm in length (Figure 3).

The pupa, which is about the size of the adult, is waxy yellow with light-orange eyes and is found in the soil (Figure 4). Table 1 summarizes the progressive changes from egg to adult.

TABLE 1. SUMMARY OF DEVELOPMENTAL STAGES OF THE LIFE CYCLE OF *Altica tombacina* (MANNERHEIM)

Stages	*No. of Examples*	*No. Days Range*	*Av.*	*Appearance*	*Measurement*
Eggs to larvae	12 batches	4-8	6	yellow cylindrical	0.6 x 0.3 mm
Larvae to pupae	100+	13-15	14		
First instar	10	2-4	3	Yellow to gray	1.5-2.0 mm
Second instar	10	3-5	4	dk. gray to black	
Third instar	10	3-8	5	shiny black	7.0 mm
Pupae to adults	100+	9-11	10	waxy yellow; eyes orange (see Table 3)	approx. same
Adults	100+		1± yr.	eyes black; body, legs, and antennae metallic bronze	3.8-4.5 mm x1.8-2.0 mm
Eggs to pupae	100+		20		
Eggs to adults	100+		30		

The adult is 3.8-4.5 mm in length and 1.8-2.0 mm in width. Its body, legs, and antennae are a metallic bronze (Figure 5). The filiform antennae have 11 segments, the third segment being shorter than the fourth. The elytron is without lateral fold. The black oval eyes in the flat head fit against the margin of the cylindrical prothorax. Beller and Hatch (1932) describe the "antebasal groove of pronotum as terminating in a shallow but sharply delimited fovea at either end."

Oviposition. The eggs are deposited in clusters of from 15 to 46 on the undersurface of the leaves of the host plant. They are laid in rows end to end in a nearly symmetrical pattern and are cemented to the lower epidermis. As shown in Table 2, one female in the laboratory produced more than 453 eggs in the 37 days between May 16 and June 22 (1961). Even though she was still alive on September 20, she laid no additional eggs after June 22.

First-generation adult females, i.e., ones which developed in the laboratory

from eggs deposited by the observational female (presumably overwintered), produced eggs from June 29 through August 18. No account was kept of the total number laid or hatched. As shown in Table 2 adults emerged throughout the summer approximately 30 days after the eggs hatched. Since the experiment terminated September 20, beetles from the last eggs oviposited were still in the pupal stage.

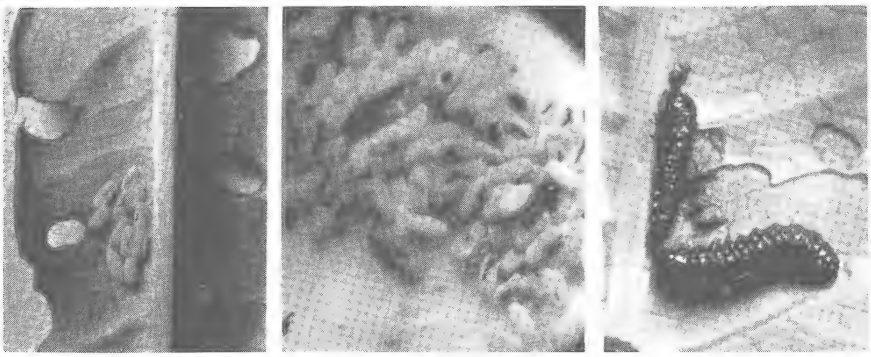
TABLE 2. OVIPOSITION BY ONE OVERWINTERED* FEMALE
(Spring and Summer 1961)

Date Eggs Deposited	*No. of Eggs*	*Dates Larvae Were Observed and No. of Larvae (in parentheses)*
May 15-16	35	May 23 (8)
May 17	15+ (combined)	May 23 (3)
May 18	15 (combined)	May 25 (20+)
May 20	15 (combined)	May 25 (20+)
May 22	15+	May 27 (some)
May 23	16	May 27 (8)-May 31 (4)
May 25-27	18	May 29-June 2 (13)
May 29	32	June 2 (27)
May 31	31	June 2-4 (some)
June 1	12	June 9 (9)-12 (1)
June 2-4	46	June 8-9 (some)
June 6	30	June 12 (5)
June 8-9	36	before June 20 (some)
June 10	10	June 20 (5)
June 12	31	June 20 (8—1-2 days old)
June 14	22	June 20-or before (16) to June 26 (3)
June 15	15	June 20 (first 1)
June 16-19	49	June 26 (some)
June 20	8	June 27 (5)
June 22	2	discarded because too dry
Total Eggs	453+	

* Presumed on basis of life-cycle observations.

No eggs were laid by second-generation beetles, leading to the assumption that second-generation beetles are the ones which hibernate and emerge in the spring to produce the next year's eggs.

Hatching. The eggs hatch in a minimum of two days, but more generally require four to eight days. Within a cluster some eggs may hatch before others begin. In one instance eight of 16 eggs laid before 9:30 a.m. on May 23 had hatched by 10:00 a.m. on May 29. On May 31, four of the



Figures 1-3. Eggs and larvae of bronze flea beetle. 1. Eggs, actual size 0.6 X 0.3 mm, laid on the undersurface of fireweed leaf. Holes were made by the feeding activities of the adult. 2. Eggs and newly hatched larvae. 3. Larvae, 7.0 mm in length and black in color, feeding on undersurface of fireweed leaf.

remaining eggs had hatched, and the others were discarded since they were moldy.

Though the newly hatched larvae have pale-yellowish bodies (Figure 2), within 24 hours they darken, ranging in color from light gray-green to dark gray or black.

Larvae feed within a few hours after hatching. They respond readily to tactile stimuli but do not move rapidly away while feeding. There are no unusual quick movements.

Molting. The different states or instars in the development of the larva are separated from one another by a molting or shedding of the larval skin as shown in Table 1. The first molt occurs within two to four days after hatching. When the larva first emerges from the old skin it is an even gray all over. Within two hours it has turned black and begun to feed again. The second molt occurs within three to five days after the first. A third molt follows in from six to eight days and initiates the beginning of pupation (see Table 1).

Pupation. The larva stops feeding and becomes less active for one to two days as it migrates from its feeding position on the plant into the soil. As pupation begins, the larval skin splits at the head and is shed from the anterior to the posterior end through longitudinal contractions and expansions of the emerging pupa, requiring about 20 hours. The only obvious movements are in the region of the abdominal segments. The pupa is slightly curled after this metamorphosis has been completed (Figure 4). Pupation lasts from nine to eleven days; the interesting changes noted during the last two days of pupation are presented in the following table.

TABLE 3. METAMORPHOSIS FROM PUPA TO ADULT

Time		last two days of the 10-day (average) pupation
No. examples		10
Place		laboratory at Linfield College
Stages:	a	body waxy yellow, eyes orange
	b	eyes red
	c	eyes black, mouth parts reddish
	d	base of antennae, wing tips, and femur-tiba joint grayish; tarsal claws reddish
	e	legs and antennae darker gray
	f	legs, antennae and mouth parts bronze; wings gray; bodily contractions
	g	thorax all bronze, elytra darker, abdomen amber yellow; beetle-shape
	h	elytra shiny bronze, abdomen trace of amber; movements to spread wings
	i	the metallic bronze adult

Adulthood. According to our observations in the laboratory, if an adult emerges in late May or June it belongs to the first generation and will lay eggs which will hatch from late June through July. The adult of the second generation apparently will not lay eggs until it appears on the host plant the following spring, presumably after hibernating in the soil all winter. More research is needed concerning the hibernation and longevity of this species.

Under natural conditions adults are first seen during the last of April or the early part of May, depending upon the weather, when fireweed plants are about six inches to a foot in height. Since there was no apparatus for simulating field conditions, the development rate of laboratory-reared insects may differ from that under natural conditions. However, in 1959, larvae reared in the laboratory on fresh fireweed leaves pupated at the same time that larvae disappeared from fireweed plants on Saddleback Mountain. Also the last adults of the year appeared at the same time in both situations.

Determination of Sex

At various times during this study specimens representative of the different stages of the life cycle from the egg to the adult were collected, some individuals were reared in the laboratory, and numerous aspects of the development of the bronze flea beetle were recorded without any males being detected by external characteristics or mating activities. It was observed when working with adults that certain nonsegregated individuals did not lay eggs, but none of the beetles produced from singly isolated pupae-laid eggs; consequently it was impossible to distinguish nonfertile females from males. However

Figures 4-6. Later life stages of bronze flea beetle. 4. Pupae, actual length approximately 4 mm, have yellow bodies and orange-colored eyes. 5. Adult beetle, on fireweed leaf. 6. Photograph of dorsal surface of the aedeagus, male genital organ, of *Altica tombacina* (highly magnified).

fertile eggs were produced by first-generation beetles which had not been isolated during the pupal stage. All of these observations led to the conclusion that the beetles had not been watched continuously enough for mating to be detected; also that development was not parthenogenetic.

Dissection for Determination of Sex. In the spring of 1964, 44 individuals from the 1961 laboratory-reared beetles were selected for microscopic dissection. Examination of their genitalia disclosed that 14 were males (Figures 6 and 7); the remainder females. Further dissection should definitely establish whether the sex ratio is one to two as it now appears to be.

No differences in external characteristics were detected except that as a rule the male is under 4 mm in length and usually the female is at least 4 mm; however, a few females under this length have been noted.

Feeding Habits

In the Saddleback Mountain research area the adults and larvae of the bronze flea beetle feed voraciously on the leaves of the fireweed plant. Essig (1958), who places *Altica evicta* LeConte as a synonym of *tombacina,* reports that it is injurious to strawberries and roses in California, Oregon, British Columbia, and Colorado. Although neither Dr. Gentner (pers. comm.) nor the Linfield research group has ever found this beetle feeding on anything but the fireweed, Kenneth Goeden, Entomologist in the Plant Division of the Oregon State Department of Agriculture, in recent correspondence recounted the following observations concerning *A. tombacina*:

> The specimens we have in our collection (23) were taken 6 miles east of Estacada feeding on Siletz strawberries. I collected the specimens on April 20, 1962, but their presence was reported to me at least two weeks earlier. The field was recently cleared of stumps and ferns typical of cutover forest land. Fireweed occurs in abundance in the bordering areas of the field. The beetles were congregated on individual berry clumps rather than as a general infestation of the entire field. Feeding damage is illustrated by the enclosed leaf (Fig. 9). I did not observe larvae at the time, although eggs, presumably flea beetle, were present. The beetles disappeared from the fields shortly after the collection date and have never been observed since.

The genus *Altica* is also listed as a minor pest of strawberries by Rosenstiel and Vaughan (1952) who state: "Both the adults and larvae skeletonize the leaves, sometimes defoliating younger plants." Mr. Goeden believes the species referred to is *A. tombacina.*

The larvae feed on the underside of fireweed leaves, removing most of

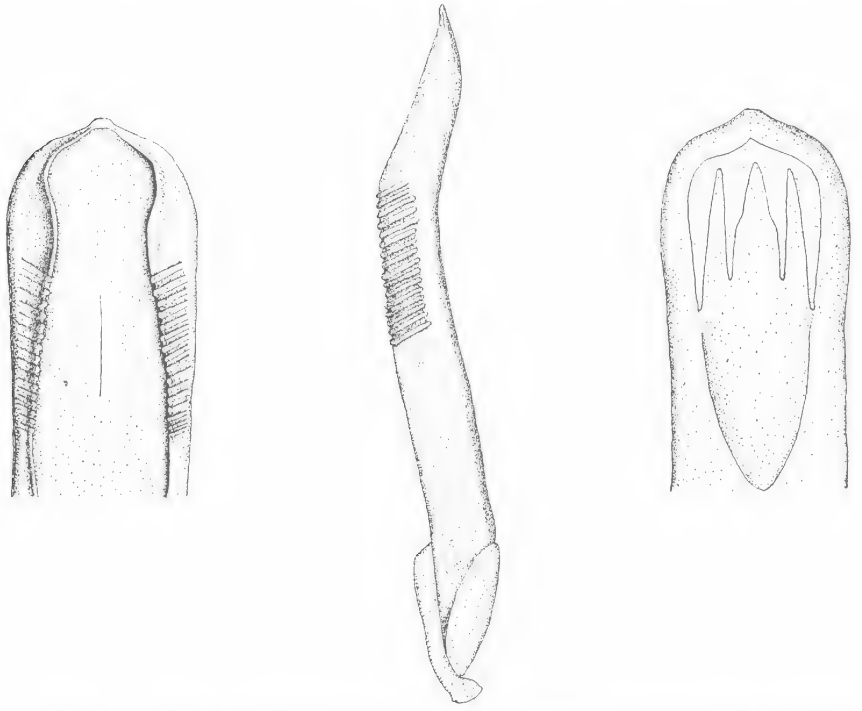
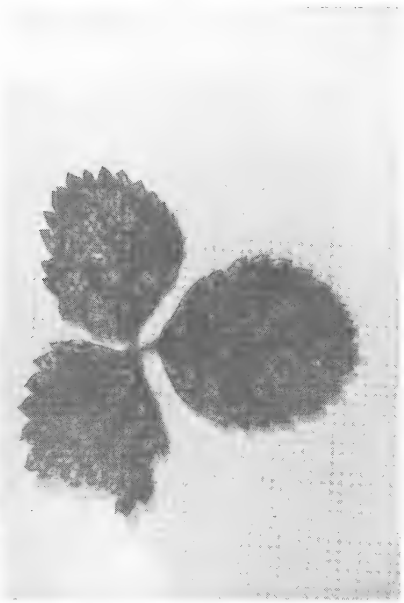


Figure 7. Detail of aedeagus, the male genital organ of the bronze flea beetle. A. Apical one half of ventral side. B. Lateral view. C. Apical one half of dorsal side. Drawings by Kenneth M. Fender.



Figures 8-9. Food plants of the bronze flea beetle. 8. Young tip of fireweed plant, *Epilobium angustifolium* L., badly damaged by feeding activities of adults. 9. Strawberry leaf, supplied by K. Goeden, showing damage by beetles of this species.

the spongy mesophyll, but according to our observations they do not eat completely through the leaf (Figure 3). One 7-mm larva was observed to remove a circular area of leaf 1 mm in diameter in three minutes with a vigorous chewing action, turning its head from side to side. In five minutes it had eaten 4 sq mm and the volume of food consumed in 13 minutes was calculated as 2 cu mm.

Both larvae and adults prefer the young and most-tender foliage. The adults, however, chew circular areas completely through the leaf, perforating them in a shot-hole-like pattern (Figures 1 and 8).

Summary

The bronze flea beetle, *Altica tombacina* (Mannerheim), is found in Alaska, British Columbia, Alberta, Washington, Oregon, California, and Colorado. On Saddleback Mountain, Oregon Coast Range, these beetles have been found feeding only on fireweed, *Epilobium angustifolium* L.; however, other investigators have reported that this species also feeds on rose leaves and strawberry leaves.

Eggs are laid in clusters, often of from 15 to 40 or more, on the under-

surface of leaves. The tiny larvae, initially yellowish, through three instars grow to 7 mm in length and turn shiny black. Larvae feed on the lower epidermis and mesophyll of the leaves while adults chew entirely through the leaves. In the soil pupae undergo a series of visible changes during the last 48 hours of pupation. No pupal skin is shed in the course of this metamorphosis.

Apparently two complete generations occur each year: one in May and early June and the second during the last of June through July. The second-generation adults lay no eggs during their first summer; therefore, it is concluded that the beetles which emerge in the spring are the second-generation adults from the preceding summer.

There are no reliable external sex characteristics to distinguish males from females. Although the male is small, usually under 4.0 mm in length and the female is 4.0-4.5 mm, small females occur occasionally. The sex ratio seems to be one male to two females, but more dissections are necessary to establish a definite ratio.

More research is needed to determine how soon the beetles start eating after emergence from pupation and, also, from hibernation.

Acknowledgements

For the painstaking observations entailed in this life history study and tabulation of data, I owe an especial debt of gratitude to three people. Nancy Myron Collins initiated the study in the fall of 1959 by rearing the first adults in the laboratory from larvae; in the fall of 1960 she noted the habits of larvae and described the metamorphosis of pupae. The details of egg-laying, larval development, and length of developmental stages were recorded by Frances W. Daniels by means of observations on laboratory-reared specimens during the summer of 1961. Dissection of adult beetles to determine presence of males and the sex ratio and summarization and analysis of data were accomplished by Rose M. Gillette.

Kenneth M. Fender kindly made the initial dissection of genitalia on one of the beetles, demonstrating the dissection technique. He also read the manuscript, making useful suggestions concerning it.

I am grateful also that Dr. Louis G. Gentner proposed the study in addition to identifying the bronze flea beetles for us. Kenneth Goeden supplied valuable information concerning feeding habits of the beetle on strawberry plants.

Thanks are due also to Howard C. Daniels and William Good for the photography used in this life history study.

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ASSOCIATION NEWS

This is the first time in recent years that *Northwest Science* is used as a news and information medium for our association. This page will be used fairly regularly to keep members informed and to provide information on the annual meetings to nonmembers who have access to this journal.

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The Research Grants Committee (Mark F. Adams, Washington State University, and Harry Caldwell, University of Idaho) wishes to announce that research grant funds are available to support research projects in the fields of natural, applied, and social sciences. The size of grants is necessarily small but any proposal for support will be given prompt consideration. Any professor, college student, or high school student may submit requests.

The request for support must include the name of the applicant, his affiliation, and in the case of high school students it must also include the name of the high school teacher. A concise statement of the proposed research project and the purpose for which the funds will be used must be included in the request. Please send your applications to the secretary-treasurer (B. V. Ettling, College of Engineering, Washington State University, Pullman, Washington 99163).

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The 39th annual meeting will be on the 15th and 16th of April, 1966, in Missoula, Montana. This will be a joint meeting with the Montana Academy of Sciences. Members will receive a call for papers in November. Persons who need extra forms for submitting titles of papers to be presented at the meeting and nonmembers who wish to present a paper may write to the secretary-treasurer at the address given above. Titles must be received by January 3, 1966, to be included in the program.

Further information on the annual meeting will appear in the February, 1966, issue of *Northwest Science.*

Edmund E. Tylutki, Associate Editor

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